DENSITY AND DISTRIBUTION OF MEIOFAUNA

IN THE NORTHEASTERN CHUKCHI SEA

By

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DENSITY AND DISTRIBUTION OF MEIOFAUNA IN THE NORTHEASTERN CHUKCHI SEA

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Abstract

Meiofaunal communities in the northeastern Chukchi Sea (Alaska) are poorly known and were investigated to determine coarse taxonomic composition, distributional patterns, and density and biomass. Core samples were taken in August through October 2012 from van Veen grabs at depths of 20-45 m, in order to assess meiofauna community structure and associations with environmental and biological variables. Overall, density and biomass were dominated by nematodes, harpacticoid copepods, and foraminifera. Total meiofaunal density (9-13 ind. cm^{-2}) was lower than in some deeper polar regions (e.g., Yermak Plateau and Nansen Basin), but generally fell within the range of published estimates for the Arctic and sub-Arctic. Total region-averaged biomass (27.4 mg C m^{-2}) was similar to estimates for the deep Arctic Makarov and Amundsen Basins, but was much lower than shallow and productive sub-Arctic regions such as the Oosterschelde estuary (North Sea, Netherlands) and intertidal areas in Kongsfjorden (Svalbard), and some Arctic locations in the Barents Sea. The ratio of meiofaunal to macrofaunal biomass (1:438) was comparable to estimates from less productive Arctic basins and from fjords, but was unexpectedly lower than other productive polar shelves (e.g., Barents Sea shelf). Regression analysis and Canonical Correspondence Analysis (CCA) ordination suggest water depth, % mud, and TOC are important predictors of nematode and harpacticoid copepod densities, whereas temperature, TOC, and macrofaunal biomass were correlated with meiofaunal community structure. These variables are proxies for the topographic control and water circulation in the region, and suggest circulation with advected nutrient input as the primary driving force behind community density and distribution patterns.

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Introduction

With greater access to the Arctic due to decreased summer ice (Stroeve et al. 2012), and increasing interest in natural resource development (Borgerson 2008), there is a need to more fully understand marine communities and the environmental drivers that structure them in order to predict and identify alterations of current community structure. Several multi-disciplinary studies in the Arctic have recently investigated marine communities from the macrobenthos to marine mammals in the northeastern Chukchi Sea, and have shown links between oceanographic circulation patterns and faunal distributions and biomass (Blanchard et al. 2013a, b; Day et al. 2013; Blanchard and Feder 2014; Ravelo et al. 2014; Schonberg et al. 2014). Biological and environmental interactions, such as increasing benthic faunal abundance with increases in organic carbon and fine-grained sediment, reflect variations in water circulation and velocity of the prominent currents of the region (Feder et al. 2005; Feder et al. 2007; Blanchard et al. 2013a, b). Heterogeneity in environmental conditions contributes to the currently observed patterns in diversity, abundance, and biomass of benthic assemblages in the Chukchi Sea (Feder et al. 1994; Feder et al. 2005, Feder et al. 2007; Blanchard et al. 2013a, b).

In the Chukchi Sea, strong pelagic-benthic coupling resulting from shallow water depths and a mismatch between primary production and planktonic grazing rates contributes to high benthic biomass (Grebmeier 1993; Grebmeier et al. 2006). Particularly high benthic biomass and density are found in areas with strong bathymetric, biological, and environmental interactions where greater concentrations of advected carbon resources are available to the benthos (Feder et al. 1994; Feder et al. 2005, Feder et al. 2007; Grebmeier 2012; Blanchard et al. 2013a, b). Recent work in the northeastern Chukchi Sea has demonstrated strong temporal and spatial covariance in macro- and megafaunal benthic communities with water depth, bottom

water temperature, sediment characteristics (e.g., grain size), and deposition of organic carbon (Feder et al. 1994; Grebmeier and Cooper 1994; Grebmeier et al. 2006; Blanchard et al. 2013a, b; Ravelo et al. 2014). From these previous studies, density and biomass of the larger size fractions of the benthos have by now been reasonably well mapped in the Chukchi Sea. There are, however, benthic components that have not been included in many of these studies, resulting in an incomplete picture of this Arctic shelf system. One of these components, meiofauna, has been neglected in many of the Arctic and sub-polar regions despite their significant contributions to food webs and nutrient recycling in general (Heip et al. 1985; Renaud et al. 2006; Fonseca and Soltwedel 2007; Giere 2009).

Meiofauna serve important functions in the ecosystem. Marine meiofauna are defined by small body size (typically 500 to 63 μm), and consist of temporary species, i.e., juvenile and larval forms of larger taxa, and permanent species, such as nematodes, harpacticoid copepods, and foraminifera, which are considered meiofauna at any life stage (Newell 1979; Giere 2009). With their small size, they are able to influence local environmental and biological conditions through burrowing and nutrient cycling, and serve as prey for other taxa (Heip et al. 1985; Renaud et al. 2006; Fonseca and Soltwedel 2007; Giere 2009). Burrowing and movement of meiofauna through the interstitial spaces in sediments brings oxygen down into the sediments, increasing microbial activity and, consequently, enhancing nutrient cycling in sediments (Coull and Bell 1979; Meysman at al. 2006; Giere 2009). The increase in bacterial biomass, in turn, may provide more food for meiofauna as well as for other taxa (Coull and Bell 1979).

Meiofaunal community structure is typically influenced by water temperature, food availability or food type, and sediment grain size (Warwick et al. 1979; Giere 2009). The community is also influenced by microbial abundance, due to their importance as food sources.

Meiofaunal biomass tends to decline with increasing latitude, which may be due to declines in microbial activity in colder waters (Wei et al. 2010). Meiofaunal density is also generally correlated with total organic carbon (TOC) content of the sediment, a proxy for food availability. Density may, therefore, increase in areas of high TOC loading, regardless of temperature (Grzelak and Kotwicki 2012). Overall, meiofaunal densities and biomass tend to be quite variable at higher latitudes, presumably associated with variable food resources and biological limitations in colder water.

High turnover rates based on short life spans and rapid reproduction of meiofauna (Giere 2009) can create high local abundance. As a result, meiofauna can outnumber macrofauna by at least 2:1, with an estimate of up to 25:1 at some locations (Newell 1979; Warwick et al. 1979; Heip et al. 1985; Kennedy and Jacoby 1999; Armonies and Reise 2000; McLachlan and Brown 2010; Bluhm et al. 2011). In the Arctic basin and North Pacific sub-polar regions, meiofauna can have high but variable densities, ranging from 9 to >400 ind. cm^{-2} (Snider et al. 1984; Soltwedel 2000). Additionally, the short generation times of permanent meiofauna can make them a significant source of secondary production, resulting in regionally high biomass (Gerlach 1971; Giere 2009). In the deep waters of the North Pacific, for example, meiofaunal biomass was greater than that of the macrofauna, with an estimated ratio of 48:1 (Snider et al. 1984). In some polar regions, meiofauna represent a large percentage of the available carbon biomass, accounting for up to ~60% of benthic faunal biomass, with ~149 mg C m^{-2} (Soltwedel 2000; Vanreusel et al. 2000; Hoste et al. 2007). In the Pacific Arctic, and the productive Chukchi Sea in particular, however, the contribution of meiofauna to total benthic biomass remains unquantified.

In this study, I investigated the meiofauna community of the northeastern Chukchi Sea to address the following questions: What is the general meiofaunal composition in the region, and is it comparable to other regions? Do meiofauna represent a significant portion of the benthic faunal carbon biomass in the northeastern Chukchi Sea? To what extent can community patterns be explained by environmental and/or oceanographic conditions? What variables best predict meiofaunal community structure?

Methods

Study area

This study was conducted as part of the Chukchi Sea Environmental Studies Program (CSESP), an interdisciplinary project investigating the biological and environmental conditions in the northeastern Chukchi Sea. Whereas the CSESP was a multi-year program, the meiofauna portion of the study was conducted for the sampling season in 2012. The 2012 CSESP area was divided into four regions, or strata, based on logistical sampling protocol for CSESP and latitudinal gradient and proximity to oil-lease/study areas. The strata for CSESP research included South (includes stations in the study area Klondike), Central A (including most of study area Burger), Central B (study area Statoil), and North (stations in Hanna Shoal). The study area is located 100 to 200 km northwest of the village of Wainwright on the northwestern coast of Alaska, and has an approximate water depth range of 20 – 45 m (Fig. 1).

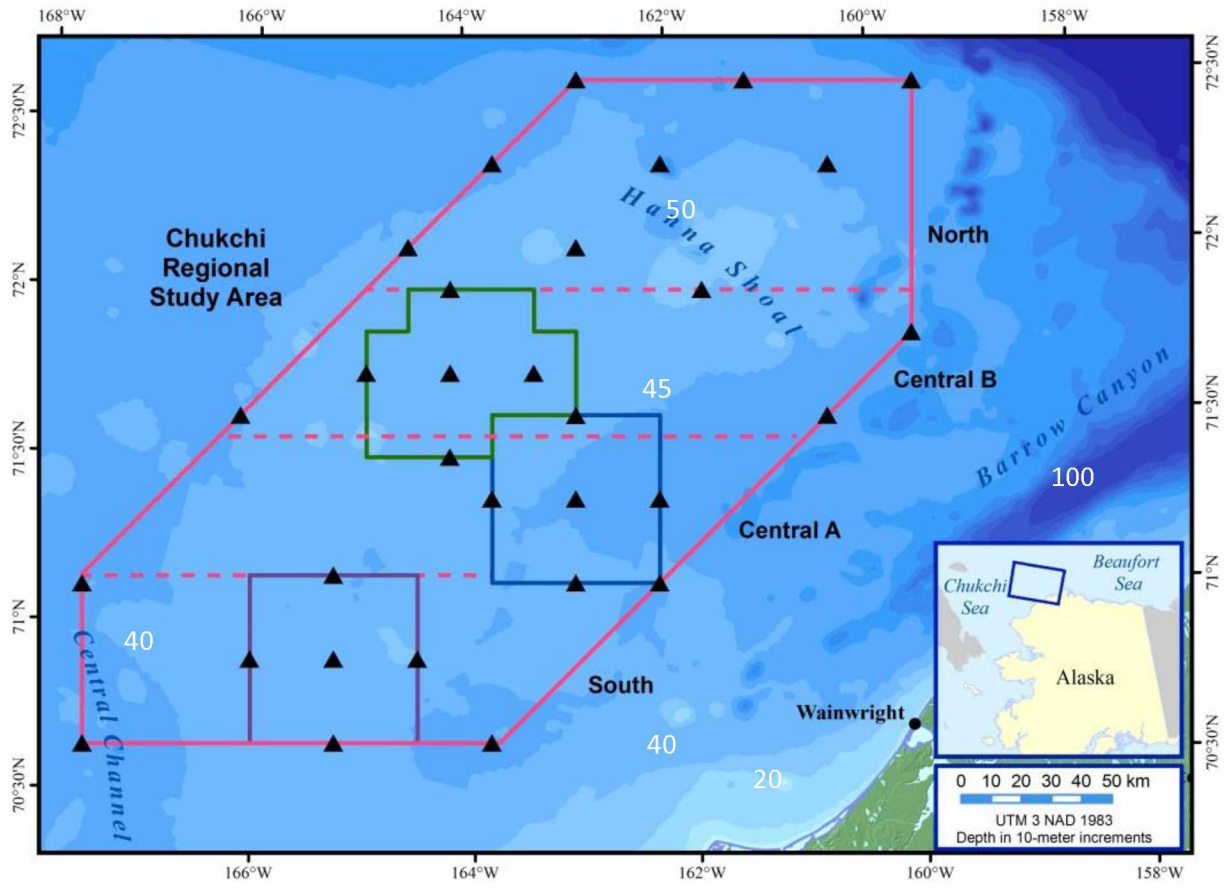


Figure 1. Study area, outlined in red, and meiofauna sampling locations from the Chukchi Sea in 2012. Colored boxes within the study area indicate main CSESP study/oil lease-sale areas (Klondike in purple, Burger in blue, and Statoil in green). Depth in the study area ranged from 20 to 50 m, depth (m) is noted in white.

Seasonal ice cover, northward currents, and shallow water depths provide ecological controls on the macro- and megabenthic communities of the area (Blanchard et al. 2013a, b). Water masses moving up through the Bering Sea into the northeastern Chukchi Sea (including the Anadyr Water, Bering Shelf Water, and Alaskan Coastal Water) advect heat, nutrients, zooplankton, and larvae of benthic fauna into the region (Fig. 2; Grebmeier et al. 2006; Blanchard et al. 2013a; Weingartner et al. 2013a). The seasonal sea ice cover is melted in part by

the influx of warmer water through the Bering Strait (Weingartner et al. 1998, 2005). Large proportions of primary production are deposited on the shallow seafloor resulting in biomass-rich benthic communities throughout the Chukchi Sea (Grebmeier et al. 2006).

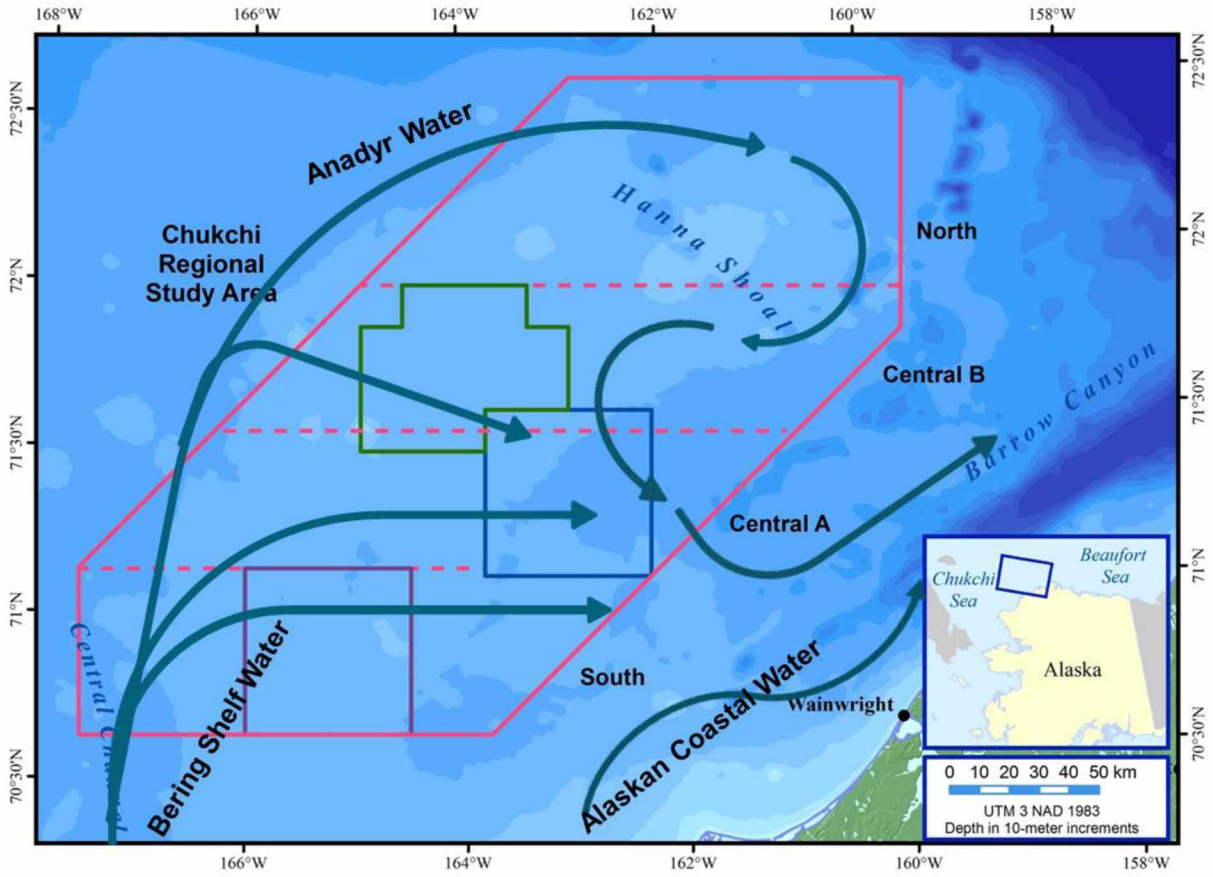


Figure 2. Conceptual diagram of water masses moving through the study area. Based on work from Winsor and Chapman (2004), Spall (2007), and Weingartner et al. (2013b); re-drawn from Tu (2013).

Seafloor topography strongly influences water mass movement in the Chukchi Sea (Weingartner et al. 1998; Weingartner et al. 2005; Spall 2007), which in turn influences environmental characteristics (e.g., TOC, % mud) and habitat heterogeneity (Feder et al. 1994;

Blanchard et al. 2013a, b). The prominent circulation of the region is as follows: Alaska Coastal Water flows along the Alaskan coast and exits the shelf via Barrow Canyon (Weingartner et al. 1998; Weingartner et al. 2005; Weingartner et al. 2013a, b). Bering Shelf Water (BSW), carrying high nutrient concentrations from the Bering Sea, branches through the lower portion of the Northeastern Chukchi Sea, with one branch exiting the shelf through Herald Canyon while another branch travels north before wrapping around Hanna Shoal and re-entering the study region from the northeast (Weingartner et al. 2005; Winsor and Chapman 2004). The branches of the BSW converge over study area Central A (near the Burger study area; Fig. 1) and water movement slows before exiting the shelf through Barrow Canyon (Weingartner et al. 2013a). The result is an environmental mosaic, with more dynamic, coarse-grained sediment environments in the south and north, and a more depositional, fine-grained, and highly productive environment closer to the Central A region (Blanchard et al. 2013a). Effects associated with the complex water circulation patterns extend throughout the ecosystem, driving differences from benthic macro- and megafauna to avian and marine mammal communities (Blanchard et al. 2013a, b; Day et al. 2013; Gall et al. 2013).

Sample collection

Sampling occurred during August to October 2012 at 31 stations (Fig. 1), with three replicate samples per station (N = 93 samples total). Density and biomass of meiofauna were estimated from sub-samples taken from the surface of a double van Veen grab (0.1 m^2 surface area per grab). A 7-cm diameter metal core was inserted into the sediment through a window on the top of the grab to a depth of 1 cm. Samples were placed in plastic bags, and preserved with 10% formalin buffered with hexamethylenetetramine. In the laboratory, samples were rinsed

over 63 and 500-µm mesh sieves (Giere 2009). The sieved samples were stained with rose Bengal and stored in isopropyl alcohol.

Following methods outlined in Burgess (2001), a silica solution separation technique was implemented to expedite the sorting process. Samples were transferred to 50-mL centrifuge tubes and the colloidal silica solution Ludox HS-40 (Sigma Aldrich, Saint Louis, Missouri) was added to each tube to equal a volume of approximately 40-45 mL of combined fluid and sediment per centrifuge tube. Each sample was mixed using a variable-speed vortex mixer at maximum speed for 30 sec, and at low speed for 4 min. Samples were subsequently transferred to a centrifuge and run at 900×*g* for 5 min. This process creates a density differential in the sample, allowing the lighter meiofaunal organisms to float to the surface. The remaining sediment was re-sorted by hand to remove any organisms not removed via the silica solution process. Once removed from the sediment, all organisms were then identified. Temporary meiofauna were generally identified to family and lower, whereas permanent meiofauna were identified to phylum. Although full taxonomic identification and diversity of permanent meiofauna was beyond the scope of this study, a subset of nematodes from eight samples (three samples from the South stratum, two from Central A stratum, and three from Central B stratum) were identified to genus level by Dr. Jyotsna Sharma at the University of Texas at San Antonio to gain insights into species composition of this numerically dominant group, which may be used for future Arctic biodiversity studies (see Appendix A).

Biomass analysis

Biomass estimates were determined for the three most abundant permanent meiofaunal taxa (nematodes, harpacticoid copepods, and foraminifera). Specimens for biomass estimates were collected from 15 additional sub-core samples (5 per the three lease-sale areas), using a 1.5

cm diameter plastic core, pushed to 5 cm depth. The cores were taken from the same van Veen grabs as the quantitative samples described above. Samples were placed in plastic bags and frozen. In the laboratory, samples were thawed and rinsed over 63- and 500-µm mesh sieves and immediately processed. All nematodes, copepods, and foraminifera were counted, removed, and placed into shell vials by taxa and stratum (e.g., one vial of nematodes for South, Central A, and Central B). Samples were then vacuum-filtered with deionized water onto pre-combusted GF/F glass microfiber filters. After filtration, samples were dried for 24 h at 60°C and subsequently placed in a vacuum chamber with 1 N HCl for 24 h to dissolve carbonates. Samples were then dried again at 60°C for 24 hours, and analyzed for mass of carbon (µg C) at the Alaska Stable Isotope Facility (ASIF), University of Alaska, Fairbanks, using a Costech Elemental Analyzer. Since multiple individuals were pooled for carbon measurement, average biomass for the study area was estimated using the average µg C per given taxon for each lease-sale area, divided by the number of individuals analyzed, resulting in an estimate of carbon mass per individual. For each taxon, the carbon mass per individual was then multiplied by the total number nematodes, copepods, and foraminifera collected at each station in order to calculate mean meiofauna biomass over each regional stratum. Estimates of biomass for each stratum were then combined to obtain an average biomass estimate for the entire study region.

Statistical analysis

In order to examine spatial patterns in meiofaunal abundance, multiple statistical approaches were used, including multiple regression to predict relationships between abundance of individual taxonomic groups and environmental and biological predictors, and canonical correspondence analysis (CCA) to determine associations between community structure and combinations of environmental and biological predictors. Analysis of variance (ANOVA) with

Tukey honest significant difference (Tukey HSD) tests were used to look at differences in abundance of individual taxonomic groups among strata, and permutational multivariate analysis of variance (PERMANOVA) of Bray-Curtis similarities was utilized to examine differences in community structure among strata using PRIMER v6 (Clarke and Gorley 2006, Plymouth Marine Laboratory). Species occurring at less than three stations with extremely low abundance (less than three individuals identified in the whole study area out of 93 samples), and fragments of organisms were removed from analyses. Data were log (x+1) transformed for community analysis.

Environmental predictors included sediment grain-size (expressed as % mud), organic carbon content of sediments (TOC), water depth, bottom-water temperature, latitude, and longitude. Temperature was highly correlated with other predictor variables % mud and depth, and was removed from regression analyses. Sediment data were taken from the macrobenthic ecology component of the 2012 CSESP (Blanchard and Knowlton 2013) and hydrographic data were provided by the physical oceanographic investigation (Weingartner et al. 2013b). Biological predictors included density and biomass of macrofaunal polychaetes, as these organisms represent the majority of fauna in the study area and are known predators of meiofauna (Fauchald and Jumars 1979; Warwick et al. 1986, Blanchard and Knowlton 2013). Response variables included meiofauna density (individuals cm^{-2}) of dominant permanent (nematodes, copepods, foraminifera) and temporary meiofaunal taxa (polychaetes, bivalves), and total meiofaunal density. Predictor variables were standardized to reduce collinearity in two-way interactions and the step function in R (R Development Core Team 2012) was used for AIC-based variable selection. CCA (from the vegan library in R; Oksanen et al. 2012) was applied to the meiofaunal species-sample matrix to evaluate how gradients of environmental and biological

variables influence meiofaunal community structure. CCA techniques visualize the responses of multiple species regressed against multiple variables in a given model, and the CCA ordination plot represents the portion of trend in the biological data accounted for by the predictors (ter Braak and Verdonschot 1995, Greenacre 2009). ArcGIS® software by Esri was used to create maps with meiofaunal density overlays.

Results

Meiofauna community structure

Meiofaunal density at each station ranged from 9 to 13 ind. cm^{-2} (Fig. 3). Permanent meiofauna in the study area occurred at densities of 1 to 10 ind. cm^{-2}. The temporary meiofauna occurred at lower densities than the permanent taxa (generally less than 1.0 ind. cm^{-2}). A total of 44 taxonomic categories were identified (Appendix B), representing organisms from 12 phyla. The majority of temporary taxa were composed of polychaetes and bivalves, which were identified to class or lower. For polychaetes, 48% were identified to family, 45% to genus, 5% to species (with 85% of those identified as the polychaete *Pholoe minuta*), and 2% were unidentified polychaete worms. For bivalves, 72% were identified to genus and 28% were unidentifiable due in part to the dissolution of shells in preservative. Of the bivalves identified to genus, >99% were *Ennucula tenuis*. Sixty-four nematode genera were identified in the 8 samples examined (Appendix A), but these taxa were not included in community structure analysis.

Spatial patterns in density and taxonomic richness were detected across the four strata within the study area, although differences were rather small. The total number of taxonomic categories identified (excluding nematode genera) was highest in Central B (31) as were average density and average number of taxa per sample (Table 1). The North stratum had the second

highest average density and the lowest average number of taxa per sample (11), which was driven by the high density of nematodes, and low density of other taxa at most of the northern stations. South and Central A were very similar in both density and number of taxa per sample.

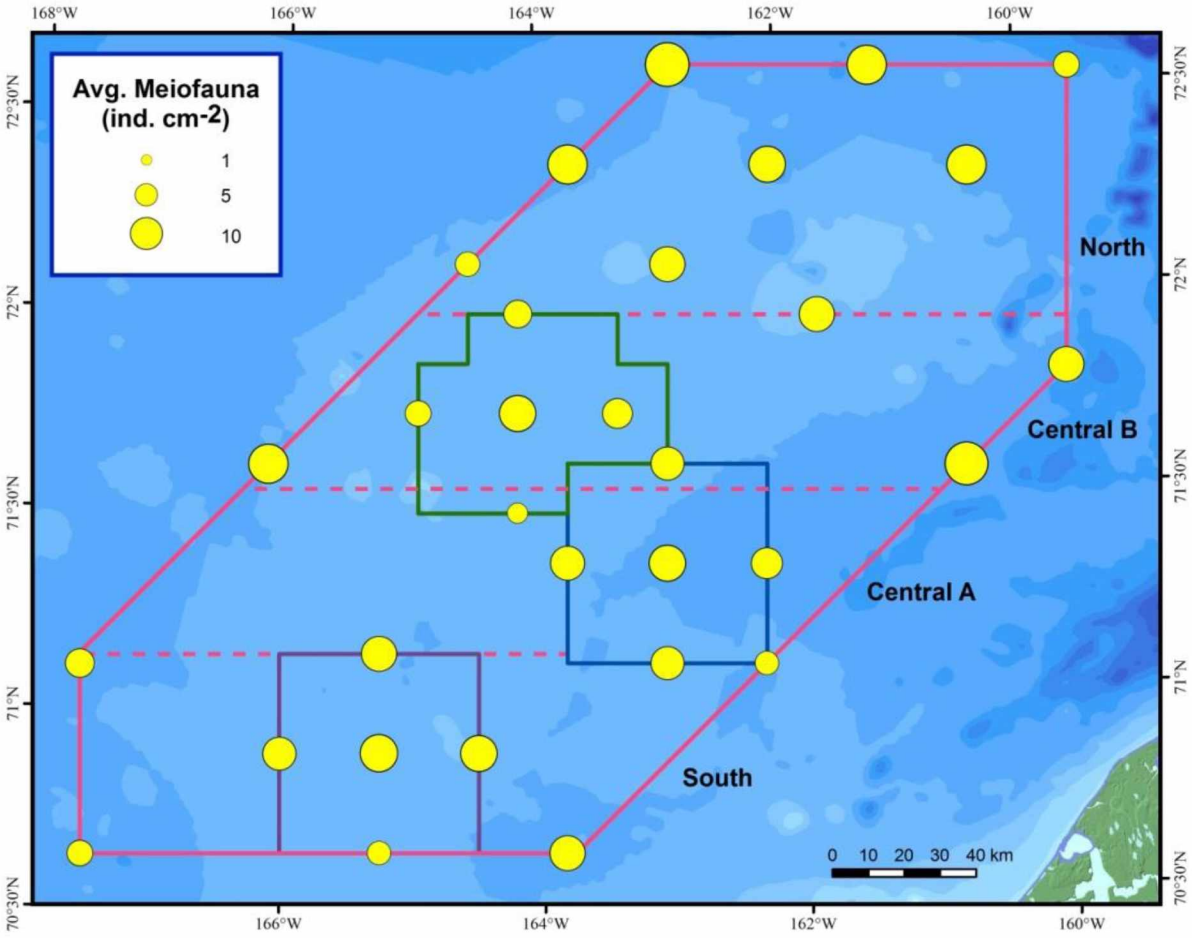


Figure 3. Density of total meiofauna (ind. cm^{-2}) from the northeastern Chukchi Sea, 2012.

Table 1. Average density (ind. cm^{-2}) and number of taxa by regional strata from the northeastern Chukchi Sea, 2012. Avg # Taxa = average number of taxonomic categories present per stratum; Total # Taxa = number of taxonomic categories found in each stratum.

Strata	Average Density	Avg # Taxa	Total # Taxa	# of Stations
South	9.5 ±1.3 SE	11.8 ±0.8 SE	27	8
Central A	9.9 ±1.0 SE	12.1 ±0.3 SE	30	6
Central B	12.9 ±1.1 SE	12.7 ±1.0 SE	31	9
North	10.2 ±1.7 SE	11.1 ±0.7 SE	30	8

Individuals were very unevenly distributed across taxa at the level taxonomically resolved. Nematodes were by far the most abundant group overall (9.0 ± 0.6 ind. cm^{-2}) and accounted for 80.6 – 88.0% of meiofauna (Fig. 4). Polychaetes (0.3 ± 0.3 ind. cm^{-2}) and foraminifera (0.2 ± 0.04 ind. cm^{-2}) accounted for approximately 4 – 7% of individuals across the study area. Copepods (0.5 ± 0.1 ind. cm^{-2}), ostracods (0.3 ± 0.1 ind. cm^{-2}), bivalves (0.2 ± 0.04 ind. cm^{-2}), and rarer taxa (e.g., tanaids and kinorhynchs, less than 0.1 ind. cm^{-2}) comprised the remainder of each community. PERMANOVA tests revealed significant differences in community structure between most strata pairs, with an overall significance of $p = 0.006$ (Table 2). Community structure in the South stratum was significantly different than both Central B and North, as was the community structure between Central A and Central B (Table 2). The meiofaunal community structure in Central B was not significantly different from the community in the North stratum. No significant differences were detected between Central A and the South or North strata.

Table 2. Permutational multivariate analysis of variance, pair-wise differences in meiofaunal community structure based on density data for the regional strata from the northeastern Chukchi Sea, 2012. Significant differences are in bold. Global p = **0.006**.

Groups	t	p-value
South, Central A	1.252	0.127
South, Central B	1.882	**0.011**
South, North	1.939	**0.010**
Central A, Central B	1.865	**0.022**
Central A, North	1.104	0.322
Central B, North	1.823	**0.043**

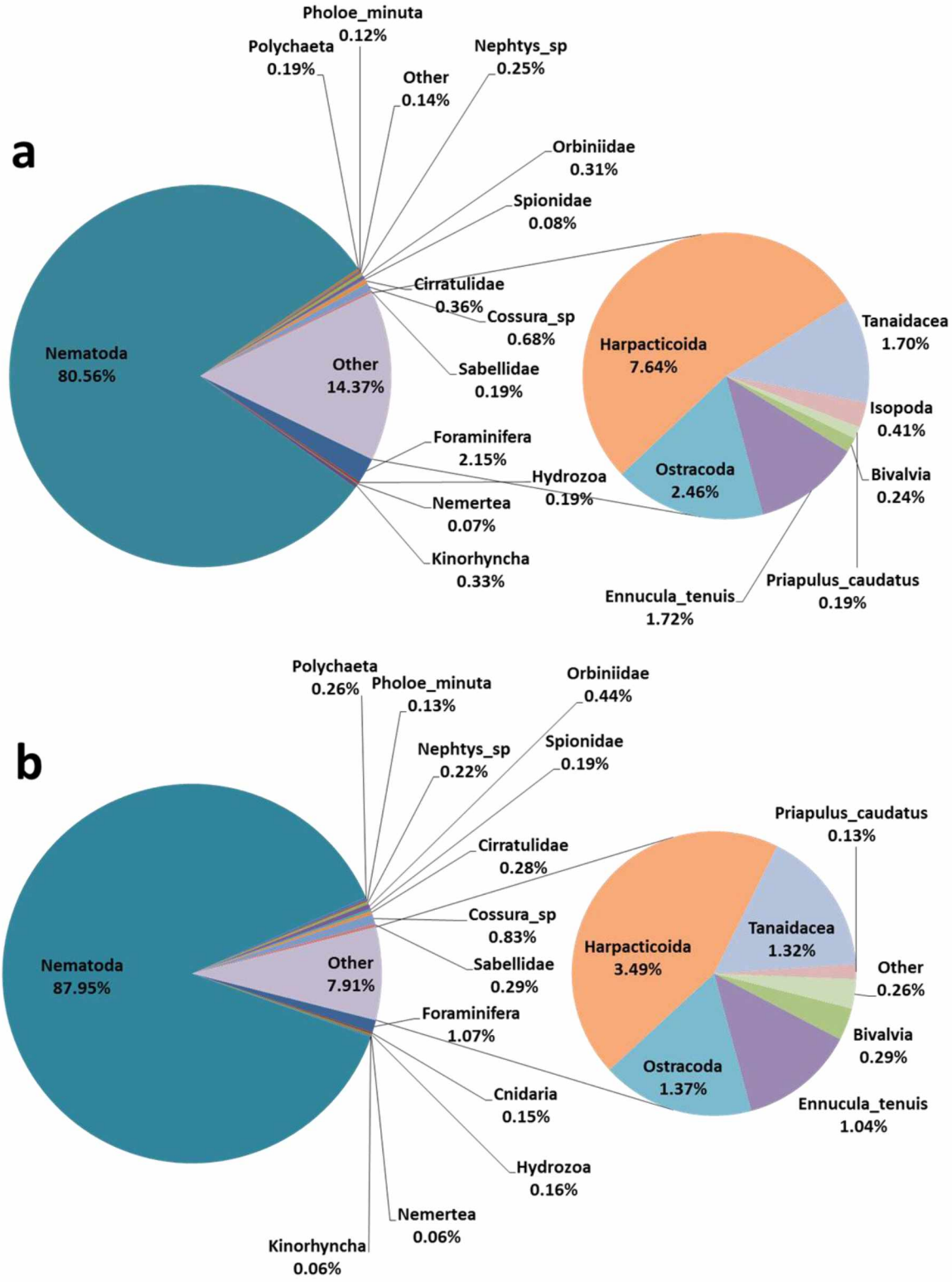


Figure 4. Community composition by density of taxa for the northeastern Chukchi Sea, 2012 (a, South; b, Central A).

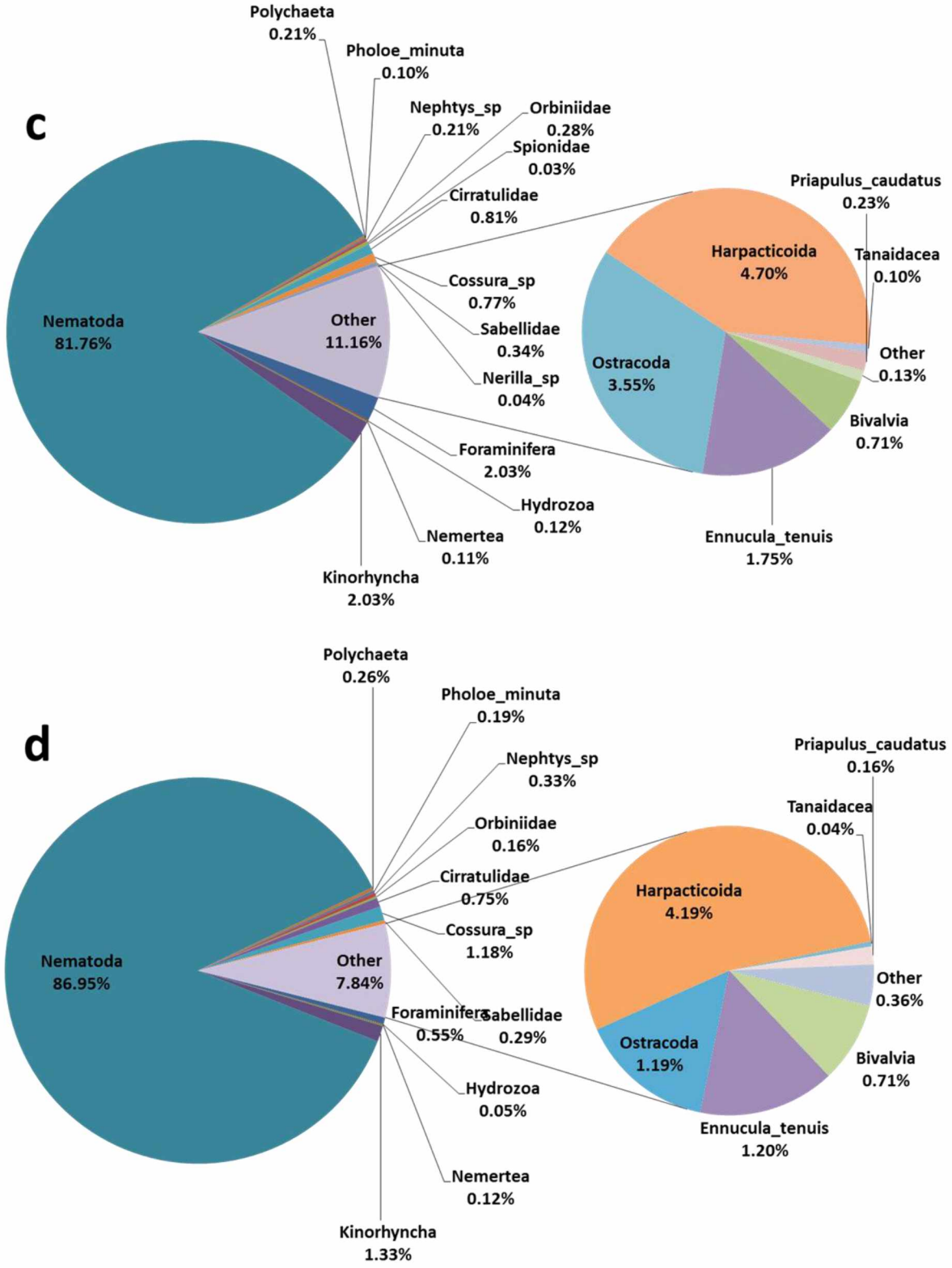


Figure 4 continued. Community composition by density of taxa for the northeastern Chukchi Sea, 2012 (c, Central B; d, North).

Several taxa exhibited differences in density between strata (Figs. 5-7). In particular, nematodes, polychaetes, ostracods, and bivalves were most abundant in Central B and had particularly low abundances in the North stratum. Across the four strata, nematodes and polychaetes shared similar distribution patterns, with low densities in the South stratum, increasing to high densities in Central B, and a sharp decrease in densities in the North. Copepods, foraminifera, ostracods, and bivalves also shared similar distribution patterns, and did not follow the same patterns as the other taxa. These groups had higher densities in the South, low densities in Central A, followed by increases in density in Central B and another sharp decrease in density in the North, however no significant regional differences were detected in these dominant groups at the 95% confidence level (Table 3; Fig. 5). At a 90% confidence level, copepods showed significant differences in density among stratum Central B and North (Table 3). Of the rarer taxa (Kinorhyncha and Tanaidacea), only tanaids showed significant differences in density among strata ($p < 0.05$), with significantly greater densities in Central B and North than in the more southern strata (Table 5, Figs. 5, 7). Although no significant differences were detected for the group Kinorhyncha, this group did display a distinct trend in density, with much lower values reported in the South/Central A regions as opposed to the Central B/North regions (Figs. 5, 7).

Table 3. Analysis of variance (ANOVA) with Tukey HSD comparisons of meiofaunal density, northeastern Chukchi Sea 2012. Non-significant terms are indicted by "--," significant terms are in bold, terms significant at $\alpha = 0.10$ are indicated with an asterisk.

Groups	Nematoda	Copepoda	Foraminifera	Ostracoda	Polychaeta	Bivalvia	Kinorhyncha	Tanaidacea
South, Central A	--	--	--	--	--	--	--	--
South, Central B	--	--	--	--	--	--	--	**<0.05**
South, North	--	--	--	--	--	--	--	**<0.05**
Central A, Central B	--	--	--	--	--	--	--	**0.04**
Central A, North	--	--	--	--	--	--	--	**0.03**
Central B, North	--	--	--	**0.07***	--	--	--	--
ANOVA *p*-value	0.31	0.33	0.19	**0.06***	0.27	0.44	0.15	**<0.05**

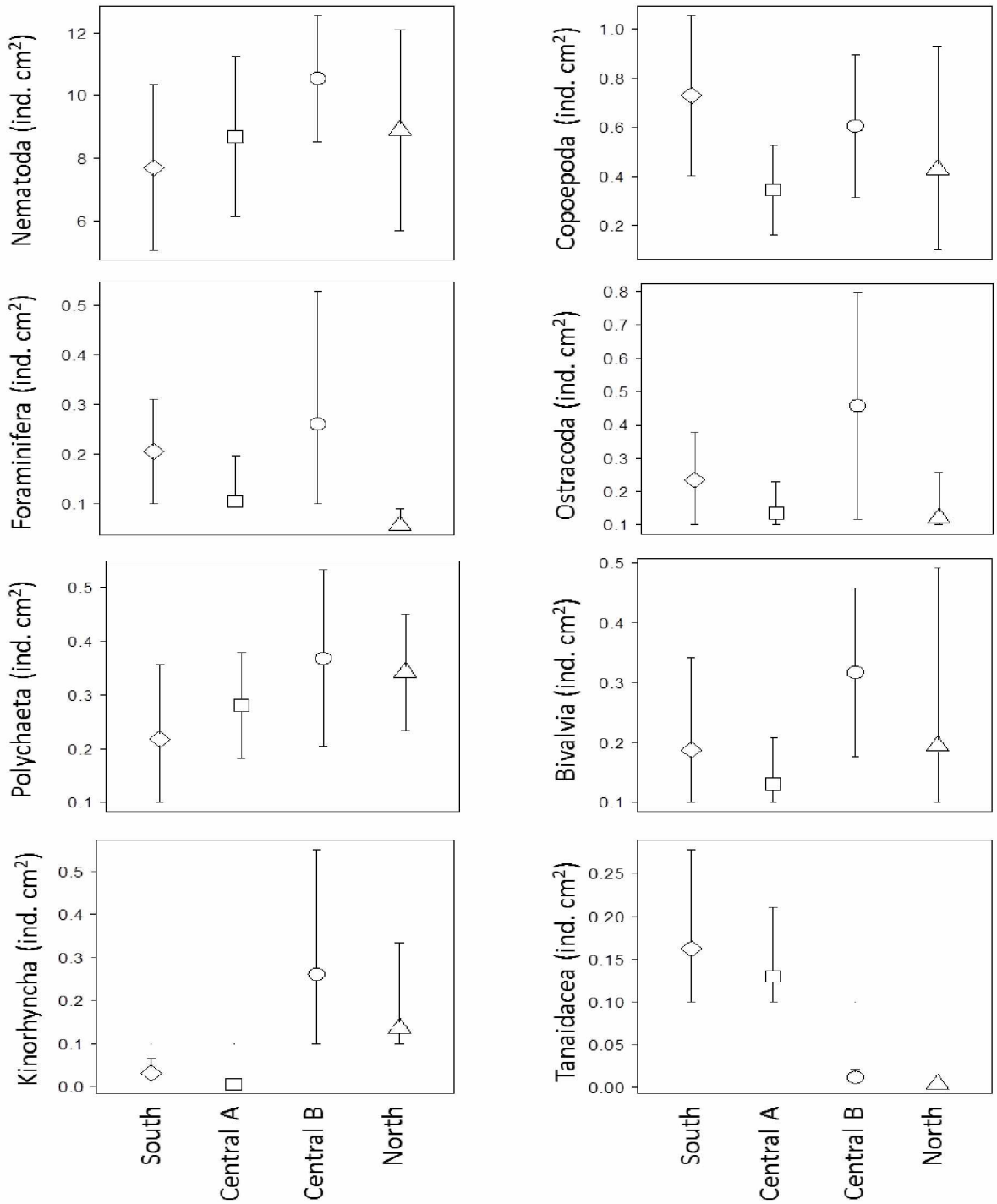


Figure 5. Mean density and 95% confidence intervals by sampling strata for major taxonomic groups and two rare groups (Kinorhyncha and Tanaidacea) from the northeastern Chukchi Sea, 2012. Note different scales, e.g., order of magnitude difference in scale for abundance of Nematodes and Tanaidacea. Significant differences are indicated in Table 3.

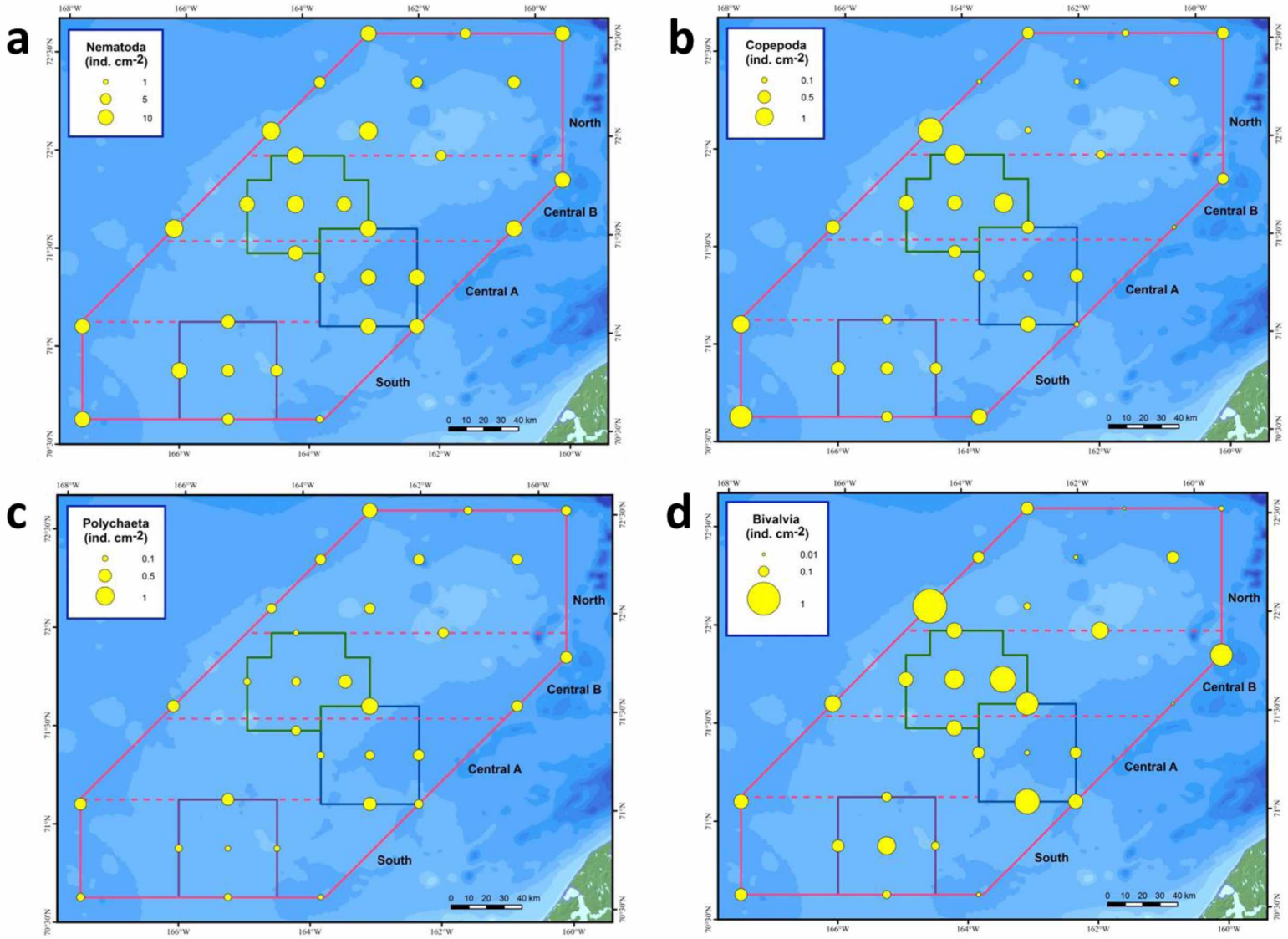


Figure 6. Density of permanent meiofauna groups a) Nematoda, b) Copepoda, and temporary meiofauna groups c) Polychaeta, and d) Bivalvia (ind. cm^{-2}) from the northeastern Chukchi Sea, 2012. Depth is colored in blue shades in 10 m increments, with darker shades indicating deeper depths.

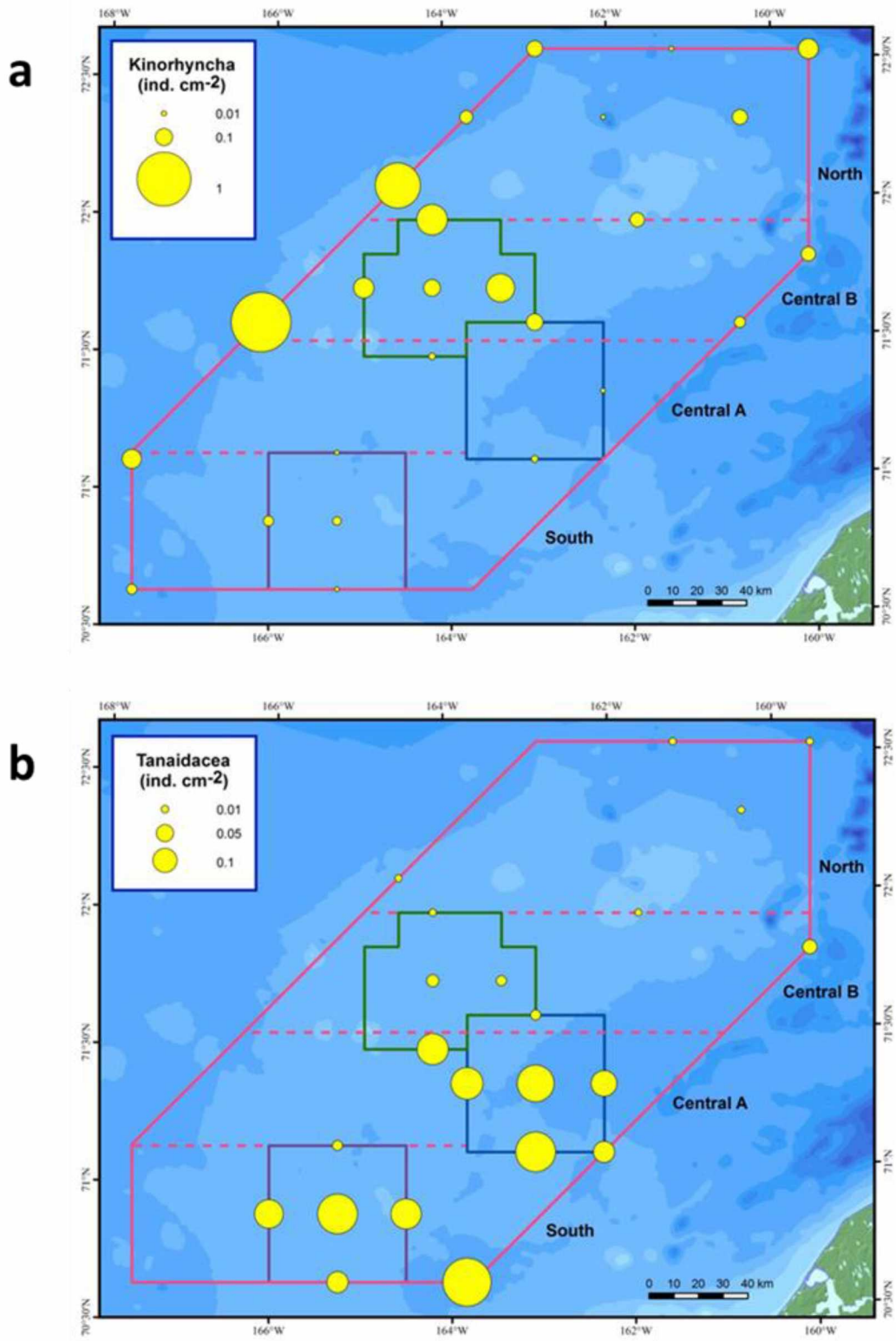


Figure 7. Density of permanent meiofaunal groups a) Kinorhyncha and b) Tanaidacea (ind. cm^{-2}) from the northeastern Chukchi Sea, 2012. Depth is colored in blue shades in 10 m increments, with darker shades indicating deeper depths.

Biomass

Meiofaunal contribution to the benthic carbon pool was inferred using values from the three most abundant (permanent) taxa, which constituted ~91% of the total meiofaunal abundance. Total average meiofauna biomass was estimated at 27.4 ± 1.7 mg C m^{-2}. Nematodes, the most abundant taxon, had the highest average biomass (19.6 ± 1.2 mg C m^{-2}), comprising 72% of the total. Harpacticoid copepods had the second highest average biomass (6.7 ± 0.96 mg C m^{-2}; 24% of total biomass) (Table 4). Foraminifera had the lowest biomass of the three groups examined, with 1.1 ± 0.3 mg C m^{-2}. Total macrofaunal biomass for the study region was estimated as 27.4 ± 1.70 mg C m^{-2} (Blanchard and Knowlton 2013).

Table 4. Average meiofaunal density (ind. cm^{-2}) across all sampling locations, northeastern Chukchi Sea, 2012; average mass per individual (µg C); and total biomass (mg C m^{-2}) across all sampling locations.

Taxa	Avg. Ind. cm^{-2}	Avg. Ind. Mass (µg C)	Total Avg. Mass (mg C m^{-2})
Nematoda	9.02 ± 0.56 SE	0.22	19.64 ± 1.22 SE
Harpacticoida	0.54 ± 0.07 SE	1.24	6.73 ± 0.96 SE
Foraminifera	0.16 ± 0.04 SE	0.65	1.06 ± 0.25 SE

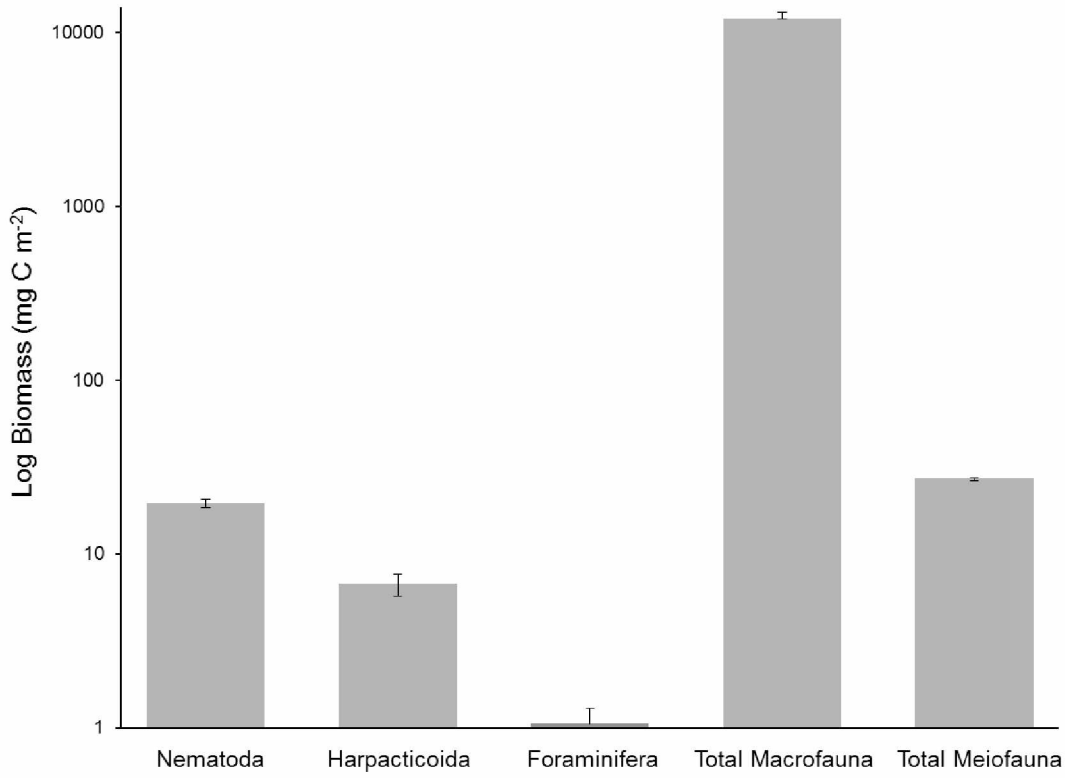


Figure 8. Log average biomass (mg C m^{-2}) for the Chukchi Sea, 2012. Macrofaunal biomass obtained from Blanchard and Knowlton (2013).

Environmental predictors of meiofauna standing stock

Regression analysis showed that % mud, latitude, and depth and their interactions were significant predictors of total meiofauna density at the 90% confidence level (Table 5). Macrofaunal (i.e., polychaete) biomass and density were not significant predictors of density for any meiofaunal groups during model selection, and were not included in final models. Total meiofaunal density was significantly influenced by interactions between depth, % mud, and latitude. These variables accounted for 25% of variance in total meiofaunal density (Table 5). Copepod density was best predicted by interactions between % mud and latitude, TOC, and depth. Fifty-six percent of variability in copepod density was captured by the measured

variables. Although ANOVA analysis for tanaids indicated the group showed significant differences in density among strata (Table 3, Fig. 5, 7), only latitude appeared to have a significant influence on predicting tanaid density. No measured variables were significant predictors of kinorhynch density (Table 5). In addition, regression analysis also did not show significant predictive results for any of the other dominant meiofaunal groups.

Table 5. Summary of results of multiple linear regressions for total meiofaunal density in the northeastern Chukchi Sea, 2012. Non-significant terms are indicted by "--," significant terms are in bold, terms significant at $\alpha = 0.10$ are indicated with an asterisk.

Variable	Total Meiofauna	Nematoda	Copepoda	Foraminifera	Ostracoda	Polychaeta	Bivalvia	Tanaidacea	Kinorhyncha
Depth	**0.01**	--	**0.01**	--	--	--	--	--	--
Mud	--	--	--	--	--	--	--	--	--
TOC	--	--	**<0.05**	--	--	--	--		--
Latitude	**<0.05**	--	**0.04**	--	--	--	--	**<0.05**	--
Depth:Mud	**0.06**	--	**<0.05**	--	--	--	--	--	--
Mud:TOC	--	--	**<0.05**	--	--	--	--	--	--
Depth:Latitude	--	--	--	--	--	--	--	--	--
Mud:Latitude	**<0.05**	--	**<0.05**	--	--	--	--	--	--
Depth:Mud:Latitude	**0.02**	--	--	--	--	--	--	--	--
Model *p*-value	**0.08***	0.13	**<0.05**	0.94	0.38	0.40	0.24	**0.04**	0.73
Overall model Adjusted r^2	0.25	0.19	0.56	0	0.04	0.03	0.11	0.30	0

Environmental predictors of community structure

CCA was used to examine the impact of environmental and biological variables on regional meiofaunal community structure based on density. Overall the CCA model accounted for ~29% of variance in the data; the first CCA axis accounted for 18% of the variance in the meiofauna community density with CCA axis 2 accounting for an additional 10% (Table 6). CCA axis 1 was moderately defined by negative correlations with temperature and macrofaunal biomass, and a positive correlation with latitude. CCA axis 2 had moderate positive correlations with predictors TOC and longitude. All other variables (% mud, depth, and macrofaunal abundance) were weakly correlated with both CCA axes.

Table 6. Canonical coefficients of environmental variables with the first two axes of a canonical correspondence analysis (CCA) for meiofaunal community density in the northeast Chukchi Sea, 2012. Moderate to high correlation coefficients (≥0.4) are printed in bold.

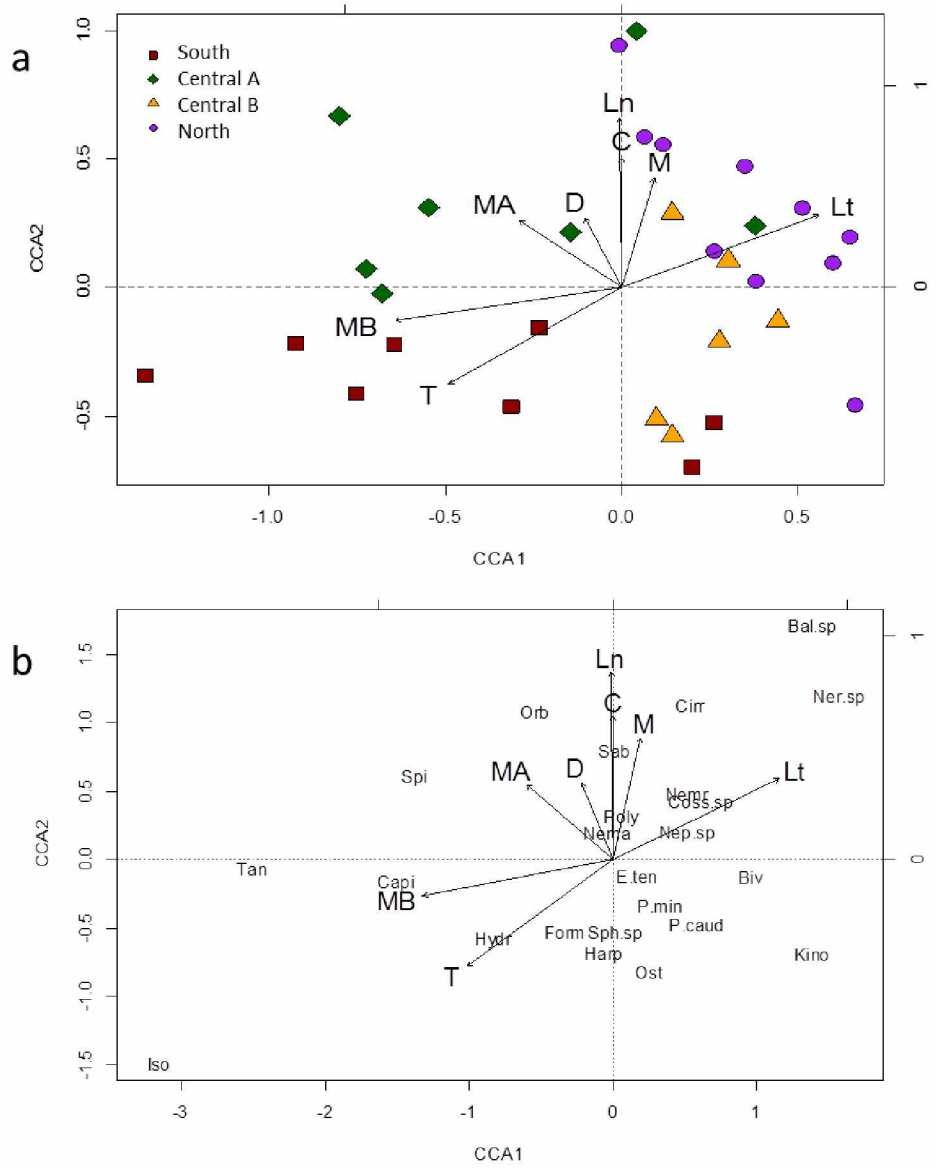
Variables	CCA1	CCA2
%Mud	0.11	0.39
Depth	-0.12	0.26
Temperature	**-0.55**	-0.34
TOC	0.00	**0.46**
Macrofaunal abundance	-0.33	0.24
Macrofaunal biomass	**-0.72**	-0.12
Latitude	**0.63**	0.26
Longitude	-0.01	**0.60**
Cumulative % variance	18.02	28.78

Looking at the meiofaunal community as a whole, distinct relationships were observed between predictors and community density using CCA. Meiofaunal density in the South stratum (red) was closely associated with high water temperature and macrofaunal biomass, lower latitude, and larger grain size (Fig. 9a). Central A stations (green) were associated with increased

water depth, latitude, TOC, and high macrofaunal abundance. Northern stations (purple) were associated with the smaller grain size, increases in latitude and TOC, as well as low macrofaunal biomass and abundance, decreased depth and temperature. Central B stations (yellow) were characterized by shallow water depth, low macrofaunal abundance and biomass, and lower temperatures (Fig. 9a).

The CCA analysis demonstrated strong associations of taxon categories with environmental and biological variables, particularly for the temporary taxa (Fig. 9b). Some polychaete taxa (e.g., *Sphaerodoropsis* sp. and *Pholoe minuta*), juvenile bivalves, kinorhynchs, and ostracods were most abundant in shallower, warmer areas, with low macrofaunal abundance. Other polychaetes (e.g., Cirratulidae, Sabellidae, *Cossura* sp., and *Nerilla* sp.) and juvenile barnacles *Balanus* sp. were also more abundant in areas with low macrofaunal biomass, particularly at higher-latitude sites characterized by low bottom-water temperature and finer grain size. Polychaetes Capitellidae, Spionidae, and Orbiniidae were correlated with high macrofauna abundance. Isopods and tanaids were associated with higher macrofaunal biomass and warmer bottom-water.

Nematodes did not demonstrate any significant associations with any of the variables tested, which resulted in their central position in the CCA. Note that in this study, nematode diversity was not resolved above phylum for the majority of samples. Nonetheless, the large number of genera identified from eight sub-samples (Appendix A) suggests that much of the resolution of the community structure analysis may have been overlooked, and environmental requirements and/or niche needs may not be reflected in CCA analyses at the phylum level.



Variables	
M = %Mud	MA = Macrofaunal abundance
D = Depth	MB = Macrofaunal biomass
T = Bottom water temperature	Lt = Latitude
C = Total organic carbon	Ln = Longitude

Taxa			
Bal.sp = Balanus sp.	Form = Foraminifera	Nemer = Nemertea	P.min = Pholoe minuta
Biv = Bivalvia	Harp = Harpacticoida	Nep.sp = Nephtys sp.	Poly = Polychaeta
Capi = Capitellidae	Hydr = Hydrozoa	Ner.sp = Nerilla sp.	Sab = Sabellidae
Cirr = Cirratulidae	Iso = Isopoda	Orb = Orbiniidae	Sph.sp = Sphaerodoropsis sp.
Coss.sp = Cossura sp.	Kino = Kinorhyncha	Ost = Ostracoda	Spi = Spionidae
E.ten = Ennucula Tenuis	Nema = Nematoda	P.caud = Priapulus caudatus	Tan = Tanaidacea

Figure 9. Canonical correspondence analysis (CCA) of log(x+1) transformed meiofaunal density. Plots are presented by stations within strata (a) and by taxon (b). Vectors indicate direction and strength of correlation between predictor variables and meiofaunal density.

Discussion

In the soft-sediments of the northeastern Chukchi Sea the composition of meiofauna was dominated by nematodes, harpacticoid copepods, and protozoan foraminifera with dominant temporary taxa contributed by polychaetes and bivalves. Abundance and biomass estimates were not unusual for the Arctic in general (Feder et al. 1994; Kröncke et al. 2000; Grebmeier et al. 2006; Giere 2009; Vanreusel et al. 2000; Wei et al. 2010) and will be discussed below. The meiofaunal biomass contribution to total benthic biomass, however, was unexpectedly low given that high concentrations of particulate organic material support high biomass of benthic macro- and megafauna in this region (Blanchard et al. 2013 a, b; Ravelo et al. 2014). Varying sub-sets of the variables bottom temperature, sediment type, sediment organic carbon content, macrofaunal biomass and water depth were associated with meiofaunal community structure (Fig. 9b), and/or contributed to the differences in density among sampling strata (Tables 2, 5). The patterns detected in the meiofaunal community reflect the influence of water circulation on benthic fauna in the northeastern Chukchi Sea.

Community composition and density

In the soft sediments of the northeastern Chukchi Sea, the composition of permanent meiofauna was dominated by nematodes, harpacticoid copepods, and protozoan foraminifera. On the phylum and order level, this taxonomic composition was generally comparable to other regions in the Arctic, sub-Arctic, and globally where nematodes and harpacticoid copepods often dominate (Table 7; Feder and Paul 1980; Soltwedel 2000; Bessière et al. 2007; Vanreusel et al. 2000; Pawłowska et al. 2011). These two groups also dominate in Arctic glacial fjords (Veit-Köhler et al. 2008, Grzelak and Kotwicki 2012), on other Arctic shelves such as the northeastern Svalbard shelf (Pfannkuche and Thiel 1987), and in the Arctic deep sea (Pfannkuche and Thiel

1987, Soltwedel et al. 2000; Hoste el al. 2007). At some shallow intertidal sites in an Arctic fjord, however, nematodes and oligochaetes were the more dominant taxa (Urban-Malinga et al. 2005). Oligochaetes appear to be restricted to low salinity habitats in the Arctic such as glacially-fed fjords (Fetzer et al. 2002) and were not found in any of the Chukchi Sea samples in 2012. Where taxa were identified on a lower taxonomic level (polychaetes and bivalves mostly), the taxa found were known from the study area and are mostly widely distributed across the Chukchi Sea (Sirenko 2001; Feder et al. 2005; Feder at al. 2007; Blanchard and Knowlton 2013; Schonberg et al. 2014). For the nematodes identified at high taxonomic resolution from a subset of samples, this study added several genera as new records for the area compared to Paul and Menzies (1974), Sirenko (2001), and Lin et al. (2014). The number of genera per sample, and throughout the region, was low (less than 20 genera per station) compared to the Chukchi slope (41genera; north-west Chukchi Sea) as well the estimated range of 30-40 genera for continental slopes worldwide (Vanreusel et al. 2000; Moens et al. 2013).

Although most taxa, at the higher taxonomic level, were widely distributed across the four strata of the study area, gradients in density and distribution patterns of several taxa resulted in differences in overall community structure, although not all were statistically significant (Tables 2, 3). Total meiofauna density ranged from 9-13 ind. cm^{-2}. This density estimate falls within reported density ranges in other areas of the Arctic and sub-Arctic, including Makarov and Amundsen Basins (10-60 ind. cm^{-2}), Adventfjorden, Spitsbergen (0.94-11.1 ind. cm^{-2}), Kongsfjorden, Svalbard (5-90 ind. cm^{-2}), and Fladen Ground, northern North Sea (<1-170 ind. cm^{-2}), (Table 7) (De Wilde et al. 1986; Vanreusel et al. 2000; Pawłowska et al. 2011; Urban-Malinga et al. 2005). Some other regions, such as Hornsund fjord (Svalbard), Nansen Basin, and Oosterschelde estuary, Netherlands, have slightly higher meiofaunal density ranges or maximum

values than the northeastern Chukchi (Table 7) (Pfannkuche and Thiel 1987; Smol et al. 1994; Soltwedel 2000; Grzelak and Kotwicki 2012). Overall, density estimates for meiofauna in the Chukchi Sea are quite similar to most current literature ranges.

Table 7. Comparison of meiofauna composition, density (ind. cm^{-2}) and biomass (mg C m^{-2}) across different regions in the Arctic, sub-Arctic, and on continental shelves. Density and biomass have been converted to carbon weight (following methods in Soltwedel 2000) when necessary, with original data and units in parentheses. WW = wet weight, DW = dry weight, ASDW = ash free dry weight. Note that differences in mesh size limit comparability to some extent.

Density (ind. cm^{-2})	Biomass (mg C m^{-2})	Area and water depth	Dominant taxa	Sampling gear and mesh size	Reference
9-13	27.4	NE Chukchi Sea (20-45 m)	Nematoda, Harpacticoida, Foraminifera	Van Veen grab, 500-63 µm	This study
--	14.9-235.6 (0.12-1.90 g WW m^{-2})	NW Barents Sea (80-240 m)	Nematodes, Harpacticoida	Multi corer, box corer, no size range given	Piepenburg et al. 1995
0.94-11.1 (942-1106 ind. 0.1 m^{-2})	3.3-21.2 (2.7-17.1 µg WW 0.1m^{-2})	Adventfjorden, Spitsbergen (70-100 m)	Nematoda, Polychaeta, Harpacticoida	Sediment corer, 500-38 µm	Pawłowska et al. 2011
20-1750 (200-17500 ind. 10 cm^{-2})	85-3527 (200-8300 µg DW 10 cm^{-2})	Oosterschelde estuary, SW Netherlands (0-41 m)	Nematoda, Harpacticoida	Box corer, 1 mm-38 µm	Smol et al. 1994
5-90 (50-903 ind. 10 cm^{-2})	124-1240 (0.2-2 g DW m^{-2})	Kongsfjorden, Svalbard intertidal (no specific depth range)	Nematoda, Oligochaeta	Multi corer, 1 mm-32 µm	Urban-Malinga et al. 2005
0.2-21 ($1.9x10^{3}$-$2.11x10^{5}$ ind. m^{-2})	0.02-20.3 ($0.164\text{-}1.54x10^{-4}$ g WW m^{-2})	N Svalbard to Makarov Basin, transect (258-4427 m)	Foraminifera, Nematoda	Box corer, 500-32 µm	Kröncke et al. 2000
0.04-0.06 (400-600 ind. $m^{-2)}$	71 mg C m^{-2}	Goban Spur, NE Atlantic (208 m)	Nematoda, Foraminifera	Box corer, 1 mm-32 µm	Flach et al. 1999
20.2	34.2 (342.3 mg C 10^{4} cm^{-2})	North Pacific (5800 m)	Nematoda, Foraminifera	Box corer, 300-42 µm	Snider et al. 1984

Table 7 continued. Comparison of meiofauna composition, density (ind. cm^{-2}) and biomass (mg C m^{-2}) across different regions in the Arctic, sub-Arctic, and on continental shelves. Density and biomass have been converted to carbon weight (following methods in Soltwedel 2000) when necessary, with original data and units in parentheses. WW = wet weight, DW = dry weight, ASDW = ash free dry weight. Note that differences in mesh size limit comparability to some extent.

Density (ind. cm^{-2})	Biomass (mg C m^{-2})	Area and water depth	Dominant taxa	Sampling gear and mesh size	Reference
10-60 (100-600 ind. 10 cm^{-2})	0.6-48 mg C m^{-2} (<1- 48 µg DW 10 cm^{-2})	Makarov and Amundsen Basins (1072-4273 m)	Nematoda, Harpacticoida	Box corer, 1 mm-32 µm	Vanreusel et al. 2000
18-320 (176-3199 ind. 10 cm^{-2})	--	Hornsund fjord, Svalbard (25-215 m)	Nematoda, Harpacticoida	Box corer, 500-38 µm	Grzelak and Kotwicki 2012
315-3955	32 (0.32 mg C 10 cm^{-2})	Yermak Plateau, Svalbard (828-3547 m)	Foraminifera, Nematoda, Harpacticoida	Multiple corer, 500-32 µm	Soltwedel et al. 2000
<1-170 (0.2-1.7x10^{6} ind. m^{-2})	1.5x10^{-4} (0.3 g AFDW m^{-2})	Fladen Ground, N North Sea (120-150 m)	Nematoda, Harpacticoida, Foraminifera	Box corer, >400 µm	De Wilde et al. 1986
23-433 (233-4339 ind. 10 cm^{-2})	17.5-119 (0.35-2.38 mg AFDW 10 cm^{-2})	Nansen Basin, SE Svalbard (226-3920 m)	Nematoda, Harpacticoida, Kinorhyncha	Box corer, 1 mm-42 µm	Pfannkuche and Thiel 1987; Soltwedel 2000

Biomass

Although biomass distribution was not resolved by region and meiofauna composition estimated only at a high taxonomic level, three major findings stand out: First, biomass was dominated by far by nematodes (Figure 8), which is in agreement with studies from other Arctic areas and from outside the Arctic (Table 7). The success of this group in the study region agrees with the global importance of nematodes in soft sediments, reflecting their tolerance to a broad range of environmental conditions, diverse feeding strategies, and high turn-over rates (Warwick 1981; Heip et al. 1985; Vanreusel et al. 2000; Renaud et al. 2006; Giere 2009). In this study, identification of nematodes was kept at phylum level. Data from the sub-sample of nematodes identified to genus (Appendix A) suggest two notions: 1) that nematode success as a group in the region is potentially due to species richness (62 genera) and the ability to fill various niches within the study area, and 2) contrastingly, the low estimate of nematode richness, compared to other shelf regions, suggests unique features of the northeastern Chukchi Sea play a role in limiting diversity of this dominant group. Potential limiting factors will be discussed in the next section.

Second, total meiofaunal biomass was generally similar to other Arctic and sub-Arctic areas, except for those from intertidal and estuarine environments (Table 7). This is likely a response to high average advected and *in situ* food supply to benthic communities on Arctic shelves in general (e.g., Piepenburg 2005), and in the Pacific-influenced Arctic (Grebmeier 2012; Nelson et al. 2014) and the northeastern Chukchi in particular (Blanchard and Knowlton 2013; Blanchard et al. 2013a). Interestingly, in areas flowing into the Chukchi (the North Pacific), and to the east of the Chukchi (the Barents Sea), meiofaunal biomass was higher than in the Chukchi (~34 mg C m^{-2} and ~43 mg C m^{-2}, respectively; Snider et al. 1984; Piepenburg et al. 1995),

which indicates that some other characteristics in the northeastern Chukchi Sea, outside of nutrients, influence the meiofaunal community.

Third, and perhaps counterintuitive to point two, meiofaunal biomass was much lower than that of macrofauna with a ratio of meiofaunal to macrofaunal biomass of 1:438. The ratio for this productive shelf is in fact similar to two rather different Arctic systems, that of the less productive Arctic deep-sea (Makarov Basin; ~1:552) (calculated from Kröncke et al. 2000) and in Arctic fjords (Pawłowska et al. 2011). This low ratio in the deep basin actually contradicts the notion that small taxa gain in relative importance over larger taxa with increasing water depth (Rex et al. 2006; Wei et al. 2010). The Chukchi Sea ratio is also similar to those in Arctic fjords in Spitsbergen (1:407 and 1:760) (Pawłowska et al. 2011), systems influenced by glacial run-off, low and variable salinities, and often high turbidity (Urban-Malinga et al. 2005). In contrast, the meio- to macrofauna biomass ratio on the productive Barents Sea shelf was much higher at 1:104 (Piepenburg et al. 1995), although the carbon resources and production rates in the Barents are similar to those in the Northeastern Chukchi (Cochrane et al. 2009; Hunt et al. 2013).

Given comparative estimates for meiofauna:macrofauna biomass ratio in the Barents Sea, questions arise as to why the ratio is lower in the Chukchi, an area similar to the Barents with respect to high nutrient resources and productivity. Low ratios of meiofaunal:macrofaunal biomass are often attributed to limited food resources, predation, and competition in less productive regions throughout the Arctic (Iken et al. 2001; Ingels et al. 2010; Pawłowska et al. 2011; Vanreusel et al. 2000). Food resources in the Chukchi, however, are not limited, as illustrated by the extensive macrofaunal community within the study area and the comparable absolute meiofauna biomass compared to other polar regions (Table 7) (Blanchard and Knowlton 2013; Blanchard et al. 2013a). Macrofaunal predators on meiofauna, although present in the

region, are nowhere near as numerically dominant as filter and deposit feeders (Blanchard and Knowlton 2013; Blanchard et al. 2013a; Schonberg et al. 2014), so it is unlikely that predation by macrofauna is limiting meiofauna. In the CSESP study area, deposit-feeding polychaete families Maldanidae, Cirratulidae, Capitellidae, and suspension-feeding Sabellidae dominate, with densities of up to ~1500 ind. m^{-2}, and biomass of over 40 g wet weight m^{-2} (Blanchard and Knowlton 2013). Their high biomass indicates these worms consume a large portion of the available food resources (Fauchald and Jumars 1979), which in part overlap with known food items for nematodes including detritus and diatom cells (Giere 2009; Guilini et al. 2010). Competition for resources with the abundant macro- and megabenthos, therefore, seems more likely as a regulating mechanism for meiofauna than macrofauna predation on meiofauna. Yet, meiofaunal density patterns were not strongly predicted by macrofauna community characteristics, and multivariate analysis resulted in conflicting associations, as the communities in South and Central A strata were correlated with higher macrofaunal biomass and abundance, whereas meiofauna in Central B (where polychaete biomass was actually the highest) was associated with low macrofaunal biomass and abundance. In light of these results, other (non-biological) parameters must also be considered as possible drivers of meiofaunal community structure in the region.

What drives meiofauna community distribution and density?

High spatial and temporal variability in density are well known for meiofaunal communities, including those in other high-latitude areas (Jewett and Feder 1977; Feder and Paul 1980; Grzelak and Kotwicki 2012). The heterogeneous distribution patterns have been explained by a suite of environmental and biological characteristics in various study systems, which included primarily sediment-related measures (e.g., grain size and TOC). For example,

communities in Port Valdez, a glacial fjord in Prince William Sound, had higher densities of nematodes in areas of finer sediment and high organic carbon, and higher densities of harpacticoid copepods in coarser sediment (Jewett and Feder 1977; Feder and Paul 1980). Grzelak and Kotwicki (2012) also found that macro- and meiofaunal communities responded similarly to changes in organic carbon input in two Spitsbergen fjords. In this study, I attempted to quantify to what extent meiofaunal community structure and density patterns can be explained by relationships to biological and environmental conditions in the Chukchi study area.

If food/resource competition between macro- and meiofauna or predation on meiofauna by macrofauna were primarily influencing the meiofaunal community (see discussion in above section), the density of dominant meiofauna would be much lower in regions of increased macrofaunal density, and much higher in regions where there are less macrofauna (i.e., the North stratum), but that is not consistently the case here. There are indeed a few predatory macrofaunal species in the region (Fauchald and Jumars 1979; Blanchard and Knowlton 2013); however, the overwhelming majority of the macrofauna, in particular the highly abundant polychaetes, are not active predators of meiofauna. Noted earlier, the dominant species are deposit or suspension feeders, so it is unlikely that predation has a large effect on the meiofaunal community, although there may be accidental or incidental consumption via burrowing, tunneling, or deposit feeding behaviors by these polychaetes (Gerlach 1978). As noted earlier, macrofauna abundance and biomass were not significant predictors of density for meiofaunal groups in the study area, and the community as a whole had a weak correlation to macrofaunal abundance. Macrofaunal distribution patterns could only partially explain meiofaunal community structure and density, while other, non-biological controls played a larger role in regulating meiofauna and are discussed next.

In general, meiofauna appear to follow roughly comparable distribution patterns as macro- and megafauna in the region. High macrobenthic and megabenthic biomass and density in the Northeastern Chukchi Sea have been tied to high food availability and strong pelagic-benthic coupling (Fig. 10) (Feder et al. 1994; 2005; 2007; Grebmeier and Cooper 1994; Grebmeier et al. 2006; Blanchard et al. 2013a; Day et al. 2013). Highest macrofaunal densities were recorded in the Central A (mean 3878 ind. m^{-2}) and Central B strata (mean 2958 ind. m^{-2}). Lowest density for macrofauna (mean 1465 ind. m^{-2}) occurred in the North. Megafauna in the region also tend to display similar distribution patterns, with higher density in areas of higher TOC, and warmer bottom water (Blanchard et al. 2013b; Ravelo et al. 2014). In general, meiofauna followed the same distribution patterns of macro- and megafauna in the region, with lower values in the North stratum (colder water, very high TOC), and higher values in Central A and B (high TOC and warmer bottom-water temperatures than the North stratum; Fig. 10). Meiofauna in the region, in particular nematodes and juvenile polychaetes, displayed similar density patterns with highest densities mostly in Central B, and mostly lower values in the North and Central A (Fig. 5).

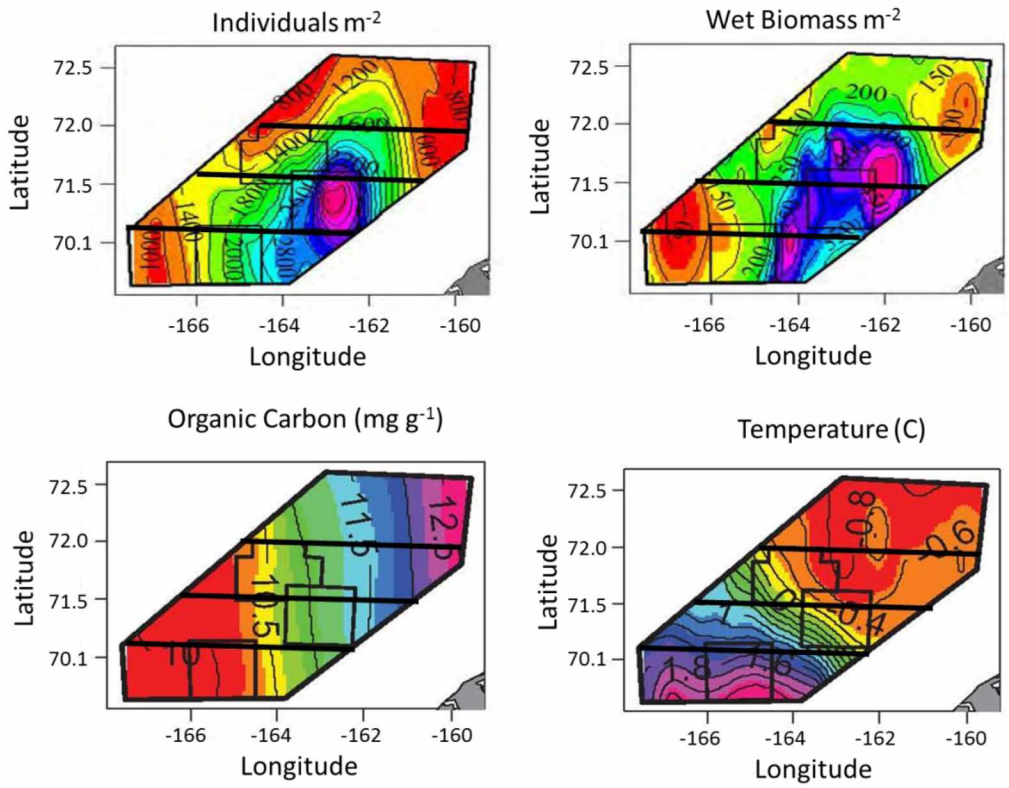


Figure 10. Spatial models of macrofaunal density and biomass, total organic carbon, and temperature from the northeastern Chukchi Sea, 2012. Reproduced from Blanchard and Knowlton 2013.

The present study identifies complexity in the interactions of meiofauna with the environment of the northeastern Chukchi Sea. Density of meiofauna is statistically associated with various combinations of hydrographic and sediment-related environmental variables as well as proxies for topography (water depth, latitude, longitude), reflecting the complex and heterogeneous sedimentary environment (Blanchard and Knowlton 2013; Blanchard at al. 2013a, b; Blanchard and Feder 2014) as well as oceanographic conditions (Weingartner et al. 2013a, b). Such complex interactions are also noted for macrofauna and megafauna of the northeastern Chukchi Sea (Feder et al. 1994; Blanchard et al. 2013a, b; Blanchard and Feder 2014; Ravelo et al. 2014).

Similarly, community structure of temporary meiofauna and most permanent taxa was also weakly to moderately associated with the environmental characteristics measured (Table 6), including varying influences of water depth, bottom water temperature, % mud, TOC, and latitude/longitude (Table 5). Combined, the first two CCA axes explained 28% of the variability in meiofaunal community structure, with most taxa preferring fine grain size, higher TOC in sediments, and shallower depths (Fig. 9a). Approximately half of the stations were correlated with warmer bottom-water temperatures.

When comparing densities between size fractions of the benthos, macrofaunal density was the lowest where TOC values were high (North stratum, 12.67 mg g^{-1}) (Blanchard and Knowlton 2013). The dominant meiofaunal taxa, including nematodes, also exhibited low density in this area (Fig. 5). Central A and B had the highest densities of macrofauna (12.9 mg C g^{-1} and 9.98 mg C g^{-1}), respectively. Central B also had the highest meiofauna density (Table 1). The range in meiofaunal abundance (9-13 ind. cm^{-2}) across the same gradient in TOC concentrations was larger than for macrofauna (0.15 - 0.30 ind. cm^{-2}); however, the only significant response to this variable was detected for harpacticoid copepods (Table 5), one of the two dominant taxa. Nematodes, the most abundant group, did not show any particular associations with TOC, and their density was not predicted by the variable. Thus, TOC content of sediments does not appear to be an important influence on total meiofaunal abundance.

It is important to note that the structure of the meiofaunal community was also associated with location as defined by latitude and longitude (Table 6; Fig. 9a). These variables, combined with changes in TOC, grain size, and bottom-water temperature, are interpreted as representing indirectly the combined effects of water circulation, topography and sea ice cover on community structure. In light of the significance of geographic location, the findings need to be placed into

context with the oceanographic conditions in the study year. In 2012, a cold winter water pool remained over the northern half of the study area (at deeper depths in mid Central A to the North stratum; Fig. 10), which was not flushed out by BSW in the area (Blanchard and Knowlton 2013). Since meiofauna have shorter longevity than macrofauna (Heip et al. 1985; Giere 2009), the community can respond faster to environmental conditions than larger fauna (Gerlach 1971; Heip et al. 1985), resulting in higher densities under favorable conditions. In this case, as warmer waters (BSW) flowed into the region, meiofauna were able to respond to the change in temperature combined with nutrient input, with increased secondary production in some areas, particularly in the Central A/Central B strata, where branches of BSW converged over the area (Grebmeier et al. 2006; Blanchard et al. 2013a; Weingartner et al. 2013a). The meiofaunal density in the North, in the cold pool, may very well represent the community as it exists for the majority of the year, with cold winter waters and thick ice cover throughout the entire region. Future studies will shed further light on the complexities of meiofauna in the northeastern Chukchi Sea

Summary and outlook

Meiofauna are an often over-looked component of the benthos, but this work shows that their inclusion in ecosystem studies provides a greater understanding of benthic systems. In the northeastern Chukchi Sea, meiofaunal density and biomass are similar to other Arctic regions, although estimates are slightly lower than some equally productive areas such as the Barents Sea shelf. The patterns in density and community structure are associated with sediment gain size, TOC, bottom-water temperature, and depth. These variables are influenced by circulation and topography of the seafloor, which resulted in the formation of cold pools that were not completely removed from the region in 2012. Meiofauna respond to environmental conditions in

the Chukchi, but clear and consistent spatial patterns for dominant taxa, and the community as a whole, were difficult to detect. The failure to detect statistically significant differences in abundance across strata could be a result of low taxonomic resolution of dominant diverse taxa (nematodes in particular) and potentially the selection of the predetermined operationally (rather than scientifically) chosen strata. Future studies might also consider targeted sampling of dominant food sources of nematodes in particular including bacteria and dissolved organic matter (Giere 2009) to aid in the interpretation of density patterns. A need remains to understand the natural variation in the meiofauna community between years and seasons in order to better understand their response to climate forcing and to distinguish responses to future human impact in the study area.

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References

Armonies W, Reise K (2000) Faunal diversity across a sandy shore. Mar Ecol Prog Ser 196:49-57

Bessière A, Nozais C, Brugel S, Demers S, Desrosiers G (2007) Metazoan meiofauna dynamics and pelagic–benthic coupling in the Southeastern Beaufort Sea, Arctic Ocean. Polar Biol 30:1123-1135.

Blanchard AL, Feder HM (2014) Interactions of habitat complexity and environmental characteristics with macrobenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. Deep Sea Res Pt II 102:132-143

Blanchard AL, Knowlton AL (2013) Chukchi Sea Environmental Studies Program 2008-2012: Benthic Ecology of the northeastern Chukchi Sea. CSESP Annual report 2013.

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013a) Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. Cont Shelf Res 67:52-66

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013b) Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009-2010. Cont Shelf Res 67:67-76

Bluhm BA, Ambrose Jr WG, Bergmann M, Clough LM, Gebruk AV, Hasemann C, Iken K, Klages M, MacDonald IR, Renaud PE, Schewe I,Soltwedel T,Włodarska-Kowalczuk M (2011) Diversity of the arctic deep-sea benthos. Mar Biodiv 41: 87-107

Borgerson SG (2008) Arctic meltdown: the economic and security implications of global warming. Foreign Aff 87:63-77

Burgess R (2001) An improved protocol for separating meiofauna from sediments using colloidal silica sols. Mar Ecol Prog Ser 214:161-165

Clarke KR, Gorley RN (2006) PRIMER V6: user manual/tutorial. Primer-E Ltd. Plymouth Marine Laboratory, 190 p.

Cochrane SK, Denisenko SG, Renaud PE, Emblow CS, Ambrose Jr WG, Ellingsen IH, Skarðhamar J (2009) Benthic macrofauna and productivity regimes in the Barents Sea—ecological implications in a changing Arctic. J Sea Res 61:222-233

Coull BD, Bell SS (1979) Perspectives of marine meiofaunal ecology. In: Livingston R J (ed.) Ecological processes in coastal and marine systems. Springer, New York, USA, pp 189– 216

Day RH, Weingartner TJ, Hopcroft RR, Aerts LAM, Blanchard AL, Gall AE, Gallaway BJ, et al. (2013) The offshore northeastern Chukchi Sea, Alaska: A complex high-latitude ecosystem. Cont Shelf Res 67:147-165

De Wilde PAWJ, Berghuis EM, Kok A (1986) Biomass and activity of benthic fauna on the Fladen Ground (northern North Sea). Neth J Sea Res 20:313-323

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol 17:193-284

Feder HM, Paul AJ (1980) Seasonal trends in meiofaunal abundance on two beaches in Port Valdez, Alaska. Syesis 13:27-36

Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitledge TE (1994) The northeastern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111:171-190

Feder HM, Jewett SC, Blanchard AL (2005) Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biol 28:402-421

Feder HM, Jewett SC, Blanchard AL (2007) Southeastern Chukchi Sea (Alaska) macrobenthos. Polar Biol 30:261-275

Fetzer I, Lønne O, Pearson T (2002) The distribution of juvenile benthic invertebrates in an arctic glacial fjord. Polar Biol 25:303-315

Flach E, Vanaverbeke J, Heip C (1999) The meiofauna: macrofauna ratio across the continental slope of the Goban Spur (north-east Atlantic). J Mar Biol Assoc UK 79:233-241

Fonseca G, Soltwedel T (2007) Deep-sea meiobenthic communities underneath the marginal ice zone of Eastern Greenland. Polar Biol 30:607-618

Gall AE, Day RH, Weingartner TJ (2013) Structure and variability of the marine-bird community in the northeastern Chukchi Sea. Cont Shelf Res 67:96-115

Gerlach SA (1971) On the importance of marine meiofauna for benthos communities. Oecologia 6:176-190

Gerlach SA (1978) Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia 33:55-69

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments, 2nd edn. Springer, Berlin, Germany, 538 pp.

Grebmeier JM (1993) Studies of pelagic-benthic coupling extended onto the Soviet continental shelf in the northern Bering and Chukchi seas. Cont Shelf Res 13:653-668

Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and Sub-Arctic Seas. Ann Rev Mar Sci 4:63-78

Grebmeier JM, Cooper LW (1994) A decade of benthic research on the continental shelves of the northern Bering and Chukchi Seas: lessons learned. In: Meehand RH, Sergienko V, Weller

G (Ed.) Bridges of Science between North America and the Russian Far East. American Association for the Advancement of Science, Fairbanks, AK, pp. 87-98

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331-361

Greenacre M (2009) Canonical Correspondence Analysis in Social Science Research. SSRN: http://ssrn.com/abstract=1435256 or http://dx.doi.org/10.2139/ssrn.1435256

Grzelak K, Kotwicki L (2012) Meiofaunal distribution in Hornsund Fjord, Spitsbergen. Polar Biol 35:269-280

Guilini K,Van Oevelen D, Soetaert K, Middelburg JT, Vanreusel A (2010) Nutritional importance of benthic bacteria for deep-sea nematodes from the Arctic ice margin: Results of an isotope tracer experiment. Limnol Oceanogr 55:1977-1989

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol 23:399-489

Hoste E, Vanhove S, Schewe I, Soltwedel T, Vanreusel A (2007) Spatial and temporal variations in deep-sea meiofauna assemblages in the Marginal Ice Zone of the Arctic Ocean. Deep Sea Res Pt I 54:109-129

Hunt GL, Blanchard AL, Boveng P, Dalpadado P, Drinkwater KF, EisnerL, et al. (2013) The Barents and Chukchi Seas: comparison of two Arctic shelf ecosystems. J Marine Syst 109:43-68

Iken K, Brey T, Wand U, Voigt J, Junghans P (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Prog Oceanogr 50:383-405

Ingels J, Van den Driessche P, De Mesel I, Vanhove S, Moens T, Vanreusel A (2010) Preferred use of bacteria over phytoplankton by deep-sea nematodes in polar regions. Mar Ecol Prog Ser 406:121-133

Jewett SC, Feder HM (1977) Biology of the harpacticoid copepod *Harpacticus uniremis* Kröyer on Dayville Flats, Port Valdez, Alaska. Ophelia 16:111-129

Kennedy AD, Jacoby CA (1999) Biological indicators of marine environmental health: meiofauna – a neglected benthic component? Environ Monit Assess 54:47-68

Kröncke I, Vanreusel A, Vincx M, Wollenburg J, Mackensen A, Liebezeit G, Behrends B (2000) Different benthic size-compartments and their relationship to sediment chemistry in the deep Eurasian Arctic Ocean. Mar Ecol Prog Ser 199:31-41

Lin R, Huang D, Guo Y, Chang Y, Cao Y, Wang J (2014) Abundance and distribution of meiofauna in the Chukchi Sea. Acta Oceanol Sin 33:90-94

McLachlan A, Brown AC (2010) The ecology of sandy shores, second edition. Academic Press, Waltham, Massachusetts, USA, 392 pp.

Meysman FJ, Middelburg JJ, Heip CH (2006) Bioturbation: a fresh look at Darwin's last idea. Trends Ecol Evol 21:688-695

Moens T, Braeckman U, Derycke S, Fonseca G, Gallucci F, Ingels J, Leduc D, et al. (2013) Ecology of free-living marine nematodes. In: Schmidt-Rhaesa A (Ed.) Handbook of zoology : Gastrotricha, Cycloneuralia and Gnathifera, Vol. 2: Nematoda. Berlin, Germany: De Gruyter, pp. 109–152

Nelson RJ, Ashjian CJ, Bluhm BA, Conlan KE, Gradinger RR, Grebmeier JM, et al. (2014) Biodiversity and biogeography of the lower trophic taxa of the Pacific Arctic Region:

Sensitivities to climate change. In: Grebemeier JM, Maslowski W (Eds.) The Pacific Arctic Region. Springer, Netherlands, pp. 269-336

Newell RC (1979) Biology of Intertidal Animals, second edition. Marine Ecological Surveys LTD, Faversham, Kent, England, 781 pp.

Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2012) Vegan: community ecology package. R package version 2.0-3. http://vegan.r-forge.r-project.org/

Paul AZ, Menzies RJ (1974) Benthic ecology of the high Arctic deep sea. Mar Biol 27:251-262

Pawłowska J, Włodarska-Kowalczuk M, Zajączkowski M, Nygård H, Berge J (2011) Seasonal variability of meio-and macrobenthic standing stocks and diversity in an Arctic fjord (Adventfjorden, Spitsbergen). Polar Biol 34:833-84

Pfannkuche O, Thiel H (1987) Meiobenthic stocks and benthic activity on the NE-Svalbard Shelf and in the Nansen Basin. Polar Biol 7:253-266

Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28:733-755

Piepenburg D, Blackburn TH, von Dorrien CF, Gutt J, Hall POJ, Hulth S, Kendall MA, Opalinski KW, Rachor E, Schmid M (1995) Partitioning of benthic community respiration in the Arctic (northwestern Barents Sea). Mar Ecol Prog Ser 118:199-213

Ravelo AM, Konar B, Trefry JH, Grebmeier JM (2014) Epibenthic community variability in the northeastern Chukchi Sea. Deep Sea Res Pt II 102:119-131

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Renaud PE, Ambrose Jr WG, Vanreusel A, Clough LM (2006) Nematode and macrofaunal diversity in central Arctic Ocean benthos. J Exp Mar Biol Ecol 330:297-306

Rex MA, Etter RJ, Morris JS, Crouse J, McClain CR, Johnson NA, et al. (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Mar Ecol Prog Ser 317:1-8.

Schonberg SV, Clarke JT, Dunton KH (2014) Distribution, abundance, biomass and diversity of benthic infauna in the northeast Chukchi Sea, Alaska: Relation to environmental variables and marine mammals. Deep Sea Res Pt II 102: 144-163.

Sirenko BI (2001) List of species of free-living invertebrates of Eurasian Arctic seas and adjacent deep waters. Russian Academy of Science, Zoological Institute, St. Petersburg, Russia

Smol N, Willems KA, Govaere JC, Sandee AJJ (1994) Composition, distribution and biomass of meiobenthos in the Oosterschelde estuary (SW Netherlands). Hydrobiologia 282:197-217

Snider LJ, Burnett BR, Hessler RR (1984) The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. Deep Sea Res 31:1225-1249

Soltwedel T (2000) Metazoan meiobenthos along continental margins: a review. Prog Oceanogr 46: 59-84

Soltwedel T, Mokievsky V, Schewe I (2000) Benthic activity and biomass on the Yermak Plateau and in adjacent deep-sea regions northwest of Svålbard. Deep Sea Res Pt I 47:1761-1785

Spall MA (2007) Circulation and water mass transformation in a model of the Chukchi Sea. J Geo Res 112: C05025 http://dx.doi.org/10.1029/2005JC002264.

Stroeve JC, Serreze MC, Holland MM, Kay JE, Malanik J, Barrett AP (2012) The Arctic's rapidly shrinking sea ice cover: a research synthesis. Climatic Change 110:1005-1027

ter Braak CJ, Verdonschot PF (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat Sci 57: 255-289

Tu K (2013) Small-scale variability in benthic food webs in the Northeastern Chukchi Sea. M.S. thesis, University of Alaska Fairbanks, Fairbanks, Alaska

Urban-Malinga B, Wiktor J, Jabłońska A, Moens T (2005) Intertidal meiofauna of a high-latitude glacial Arctic fjord (Kongsfjorden, Svalbard) with emphasis on the structure of free-living nematode communities. Polar Biol 28:940-950

Vanreusel A, Clough L, Jacobsen K, Ambrose W, Jivaluk J, Ryheul V, Herman R, Vincx M (2000) Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. Deep Sea Res Pt I 47:1855-1879

Veit-Köhler G, Laudien J, Knott J, Velez J, Sahade R (2008) Meiobenthic colonisation of soft sediments in arctic glacial Kongsfjorden (Svalbard). J Exp Mar Biol Ecol 363:58-65

Warwick RM (1981) The influence of temperature and salinity on energy partitioning in the marine nematode *Diplolaimelloides bruciei*. Oecologia: 318-325

Warwick RM, Joint IR, Radford PJ (1979) Secondary production of the benthos in an estuarine environment. In: Jefferies RL et al. (Ed.) Ecological processes in coastal environments: The 1st European Ecological Symposium and 19th Symposium of the British Ecological Society, Norwich, 12-16 September 1977, pp 429-450

Warwick RM, Gee JM, Berge JA, Ambrose Jr W (1986) Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. Sarsia 7:11-16

Wei CL, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T, et al. (2010) Global patterns and predictions of seafloor biomass using random forests. PLoS ONE 5(12): e15323. doi:10.1371/journal.pone.0015323

Weingartner TJ, Cavalieri DJ, Aagaard K, Sasaki Y (1998) Circulation, dense water formation, and outflow on the northeast Chukchi shelf. J Geophys Res Oceans 103:7647-7661

Weingartner T, Aagaard K, Woodgate R, Danielson S, Sasaki Y, Cavalieri D (2005) Circulation on the north central Chukchi Sea shelf. Deep Sea Res Pt II 52:3150-3174

Weingartner T, Dobbins E, Danielson S, Winsor P, Potter R, Statscewich H (2013a) Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. Cont Shelf Res 67:5-22

Weingartner T, Dobbins E, Danielson S, Winsor P, Potter R, Statscewich H (2013b) Physical oceanographic measurements in the Northeastern Chukchi Sea: 2012. CSESP Annual report 2013.

Winsor P, Chapman DC (2004) Pathways of Pacific water across the Chukchi Sea: A numerical model study. J Geophys Res Oceans 109: C03002. doi:10.1029/2003JC001962

Appendix A

List of Nematode Taxa Identified for the Northeastern Chukchi Sea, 2012

ENOPLIA

ENOPLIDAE

Enoplus

THORACOSOOMOPSIDAE

Enoploides

Mesacanthion

Oxyonchus

Saveljevia

PHANODERMATIDAE

Crenopharynx

Micoletzkyia

Phanodermopsis

ANTICOMIDAE

Anticoma

LEPTOSOMATIDAE

Platycoma

OXYSTOMINIDAE

Halailaimus

Oxystomina

Thalassolaimus

ONCHOLAIMIDAE

Filioncholaimus

Metoncholaimus

Oncholaimus

Phylloncholaimus

Pontonema

Viscosia

ENCHELIDIIDAE

Bathyeurystomina

Eurystomina

TRIPLONCHIDA

RHABDODEMANIIDAE

Rhabdodemania

TREFUSIIDAE

Rhabdocoma

CHROMADORIDA

CHROMADORIDAE

Acantholaimus

Chromadorita

Dichromadora

Hypodontolaimus

Prochromadorella

Spiliphera

SELACHINEMATIDAE

Halichoanolaimus

CYATHOLAIMIDAE

Longicyatholaimus

Metacyatholaimus

MICROLAIMIDAE

Microlaimus

Molgolaimus

MONHYSTERIDA

XYALIDAE

Daptonema

Monhystrium

Paramonhystera

Pseudosteineria

Thalassomonhystera

Theristus

SCAPTRELLIDAE

Scaptrella

SPHAEROLAIMIDAE

Sphaerolaimus

Parasphaerolaimus

Metasphaerolaimus

SIPHONOLAIMIDAE

Siphonolaimus

LINHOMOEIDAE

Disconema

Terschellingia

Eumorpholaimus

Linhomoeus

Metalinhomoeus

Megadesmolaimus

Paralinhomoeus

AREOLAIMIDA

AXONOLAIMIDAE

Axonolaimus

COMESOMATIDAE

Cervonema

Hopperia

Sabatieria

Sabatieria sp. 2

Sabatieria sp. 3

S. hilarula cf.

Metacomesoma

Paramesonchium

Dorylaimopsis

DIPLOPELTIDAE

Diplopeltoides

Southerniella

Appendix B

List of Meiofaunal Taxa Collected in the Northeastern Chukchi Sea, 2012

PROTOZOA
- FORAMINIFERA

CNIDARIA
- HYDROZOA
  - Corynidae
    - *Sarsia* sp.

BRYOZOA

NEMERTEA

KINORHYNCHA

NEMATODA

ANNELIDA
- POLYCHAETA
  - Pholoidae/Sigalionidae
    - *Pholoe minuta*
  - Nephtyidae
    - *Nephtys* sp.
  - Sphaerodoridae
    - *Sphaerodoropsis* sp.
    - *Sphaerodoropsis minuta*
    - *Sphaerodoropsis sphaerulifer*
  - Lumbrineridae
    - *Lumbrineris* sp.
  - Dorvilleidae
  - Orbiniidae
  - Chrysopetalidae
    - *Dysponetus pygmaeus*
  - Paraonidae
    - *Aricidea* sp.
  - Apistobranchidae
  - Spionidae
    - *Polydora* sp.
  - Cirratulidae
  - Cossuridae
    - *Cossura* sp.
  - Flabelligeridae

- Scalibregmidae
  - *Scalibregma californicum*
- Capitellidae
- Maldanidae
- Pectinariidae
  - *Pectinaria hyperborea*
- Ampharetidae
- Trichobranchidae
  - *Terebellides stroemi*
- Sabellidae
- c.f. Nerillidae
  - *Nerilla* sp.

MOLLUSCA

- GASTROPODA
  - Buccinoidea
    - *Buccinum polare*
- BIVALVIA
  - Nuculidae
    - *Ennucula tenuis*
  - Yoldiidae
    - *Yoldia* sp.

PYCNOGONIDA

CRUSTACEA

- OSTRACODA
- COPEPODA
  - Harpacticoida
- CIRRIPEDIA
  - Balanidae
    - *Balanus* sp.
    - *Balanus* sp. cyprid
- TANAIDACEA
- ISOPODA

CEPHALORHYNCHA

- PRIAPULIDAE
  - *Priapulus caudatus*

ECHINODERMATA

- HOLOTHUROIDEA